Taxonomía, Sistemática y Filogenia de la Familia Syllidae (Annelida, Polychaeta)

Resumen

Esta tesis se ha centrado en cuatro temas que precisaban de revisión en la biología de la familia Syllidae. La primera parte es una revisión taxonómica de colecciones de sílidos no identificados de áreas poco conocidas en todo el mundo con el fin de caracterizar la fauna y de resolver algunas lagunas taxonómicas. La segunda parte es una revisión actualizada de los géneros poco conocidos, para determinar qué géneros son válidos, y caracterizar la diversidad morfológica en la familia. La tercera parte incluye una revisión global de la filogenia de Syllidae basada en datos moleculares y morfológicos. Las relaciones entre los principales grupos dentro de Syllidae y la evolución de los modos de reproducción se investigan y se discuten en esta sección. Por último, la cuarta parte propone una nueva clasificación para Syllidae con el objetivo de permitir la utilización práctica de toda la información alcanzada en las partes anteriores.

Palabras clave: Polychaeta, Annelida, Phyllodocida, Syllidae, taxonomía, sistemática, filogenia, cladística, evolución, clasificación, especie, familia, géneros, diagnosis, clave dicotómica, distribución.

Taxonomy, Systematics and Phylogeny of the Family Syllidae (Annelida, Polychaeta)

Abstract

The scope of this thesis has focused in four topics for which a revision urged in the biology of the family Syllidae. The first part is a taxonomic review of collections containing unidentified syllids from poorly known worldwide areas in order to characterize the fauna and to solve some taxonomical nuisances. The second part is an update of poorly known genera in order to determine which genera are valid, and to characterize the morphological diversity in the family. The third part involves a global revision of the phylogeny of Syllidae based on molecular and morphological data. The relationships between the principal groups within Syllidae and the evolution of the reproductive modes are tested and discussed in this section. Finally, the fourth part addresses a new classification for the Syllidae aiming to allow a practical use of all the information achieved in the previous parts.

Key words: Polychaeta, Annelida, Phyllodocida, Syllidae, Taxonomy, sistematics, phylogeny, cladistics, evolution, classification, species, family, genera, diagnosis, dichotomic key, distribution.

Taxonomía, Sistemática y Filogenia de la Familia Syllidae (Annelida, Polychaeta)

Tesis doctoral

María Teresa Aguado Molina

UNIVERSIDAD AUTONOMA
DE MADRID

TAXONOMÍA, SISTEMÁTICA Y FILOGENIA DE LA FAMILIA SYLLIDAE (ANNELIDA, POLYCHAETA)

Tesis doctoral

María Teresa Aguado Molina

Memoria presentada para la obtención del título de Doctora en Ciencias con la mención de Doctor *Europaeus*

Dirigida por el Dr. Guillermo San Martín

Departamento de Biología
Unidad de Zoología

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Dissertation presented for the PhD degree in Sciences with the Doctor *Europaeus* Mention

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Taxonomy, systematics and phylogeny of the Family Syllidae (Annelida, Polychaeta)

Abstract

The Syllidae is one of the largest families of polychaetes comprising a high number of species and genera. Although syllids are highly diversified and occur in practically all benthic habitats, some aspects of their systematics remain elusive. New species and genera are continuously being described but the evolutionary relationships between them are still poorly characterized, and there are numerous geographical areas in which Syllids have not been studied so far. Thus, the current classification into four subfamilies (Syllinae Grube, 1850; Exogoninae Langerhans, 1879; Eusyllinae Malaquin, 1893; and Autolytinae Langerhans, 1879) remains in use yet solely for practical reasons because, in effect, it is not a phylogenetic hypothesis properly. The scope of the present thesis has focused in four topics for which a revision urged in syllid biology.

The first part is a taxonomic review of collections containing unidentified syllid material from poorly known worldwide areas, such as Panama, Japan, Indonesia, California and Lebanon. In this part we characterize the syllid fauna from these areas, but also solve taxonomical nuisances. The second part is an update of poorly known genera which were described during the beginning of the Twentieth century, and whose descriptions in most of the cases were incomplete. The principal objective in this second part was to determine which genera are valid, and to characterize the morphological diversity in the family. The third part involves a global revision of the phylogeny of Syllidae based on molecular and morphological data. The relationships between the principal groups within Syllidae and the evolution of the reproductive modes are tested and discussed in this section. Finally, the fourth part addresses a new classification for the Syllidae aiming to allow a practical use of all the information achieved in the previous parts.

Within the first part a total of 10 new species from Japan, Indonesia and California are described; the diagnosis of three different genera are modified stating the principal morphological features and their variability; several comparative tables with all the species on each genera are included; several new combinations are proposed following the rules of the

International Code of Zoological Nomenclature; numerous species are firstly reported for the prospected areas; additional morphological features, not previously characterized for different species are also described; several synonymies are recognized and others previously proposed are considered invalid, re-describing the correspondent taxa; several species complexes are identified; hypotheses about possible migratory paths to the Mediterranean are also proposed; and finally, different hypotheses explaining the appearance of morphological features in some species are related to the habitat in which they leave (e. g. interstitial, sponges or corals).

In the second part several type series of unusual and poorly known genera of Syllidae are examined. New diagnoses for the following genera: *Anguillosyllis* Day, 1963, *Clavisyllis* Knox, 1957, *Lamellisyllis* Day, 1960 and *Nuchalosyllis* Rullier & Amoureux, 1979, and re-descriptions of their type species are provided. *Brachysyllis* Imajima & Hartman, 1964, previously synonymized with *Dioplosyllis* Gidholm, 1962, is considered to be a valid taxon, and the species *Brachysyllis infuscata* Ehlers, 1901 is re-described. Three genera are considered to be non-valid taxa: *Braniella* Hartman, 1964, *Alluaudella* Gravier, 1905, and *Exogonella* Hartmann, 1961 for being synonymous with *Odontosyllis* Claparède, 1863 *Anguillosyllis* and *Paraexogone* Mesnil & Caullery, 1918, respectively. Finally, *Exogonoides* Day, 1963 is considered *nomina dubia* since its relationships with syllids could not be established.

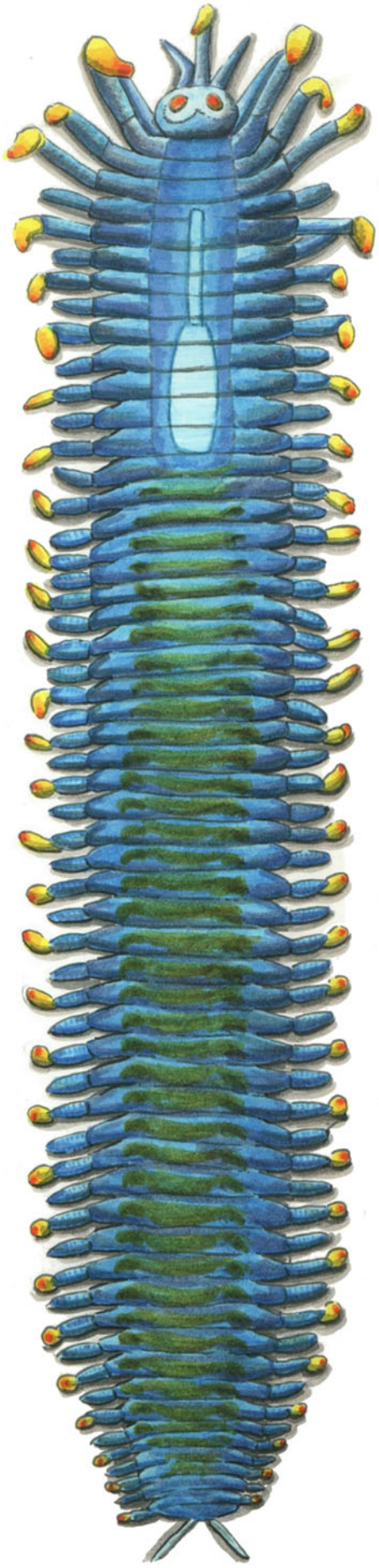
The third part comprises three phylogenetic analyses; the first one is based on molecular data and two others are based on morphological information. In the first study the phylogeny of Syllidae is assessed in a combined analysis of molecular data from nuclear 18S rDNA and mitochondrial 16S rDNA and cytochrome *c* oxydase subunit I. Eighty eight syllids in total of the four classical subfamilies Eusyllinae, Exogoninae, Syllinae and Autolytinae are included, as well as 15 outgroup taxa from Phyllodocida and Eunicida. A maximum parsimony analysis of the combined data sets indicates that Syllidae is monophyletic although not highly supported. The subfamilies Autolytinae, Syllinae and Exogoninae are monophyletic, although Exogoninae is not well supported and Eusyllinae is clearly paraphyletic. The genera *Astreptosyllis* Kudenov and Dorsey, 1982, *Streptosyllis* Webster and Benedict, 1884 and *Syllides* Örsted, 1845 comprise a monophyletic group well differentiated from the rest of the Syllidae.

The phylogeny of Syllidae is also assessed in two parsimony analyses of 111 morphological characters each. All the 64 genera currently valid for the family are included in

the first analysis as well as members of other families of Phyllodocida. In the second analysis 19 poorly known genera are excluded. Both analyses provide similar results than the previous molecular analysis in finding three of the four subfamilies as monophyletic (Exogoninae, Syllinae and Autolytinae), while Eusyllinae is clearly paraphyletic.

However, the monophyletic condition of the family is not fully resolved. Results also indicate high levels of homoplasy in the morphological characters traditionally used in the group. The evolutionary relationships between the two principal reproductive modes in the family, epigamy -where the whole animal is involved, and schizogamy -where stolons are developed from the posterior end, are elucidated. All the analyses (molecular and morphological ones) coincide in that epigamy is the plesiomorphic condition, while schizogamy might have appeared independently in Autolytinae and Syllinae. In addition, Exogoninae may be divided in two monophyletic groups attending to the dorsal and ventral brooding system.

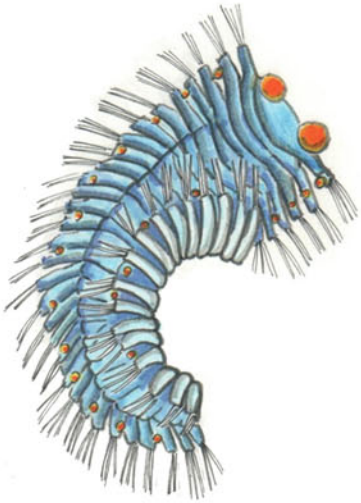
Finally, a new classification for the family Syllidae is provided in the fourth part. This classification summarizes all the recent improvements about systematics and evolution on syllids achieved in this volume. Three of the traditional subfamilies are maintained (Autolytinae, Syllinae and Exogoninae) since they were proven to be monophyletic in the previous phylogenetic analyses. In addition, one further monophyletic group is proposed as a new subfamily, the Anoplosyllinae. The name “eusyllinae”, although lacking taxonomic rank, is maintained because it embraces several genera that might be another natural group. Several genera whose phylogenetic relationships are still uncertain are included within the “*incertae sedis*” until new results allow us to clarify their relationships. Diagnoses of all recognized genera together with a catalogue with all valid species are all included.



A Jesús

y

a mis padres
y hermanos



ÍNDICE

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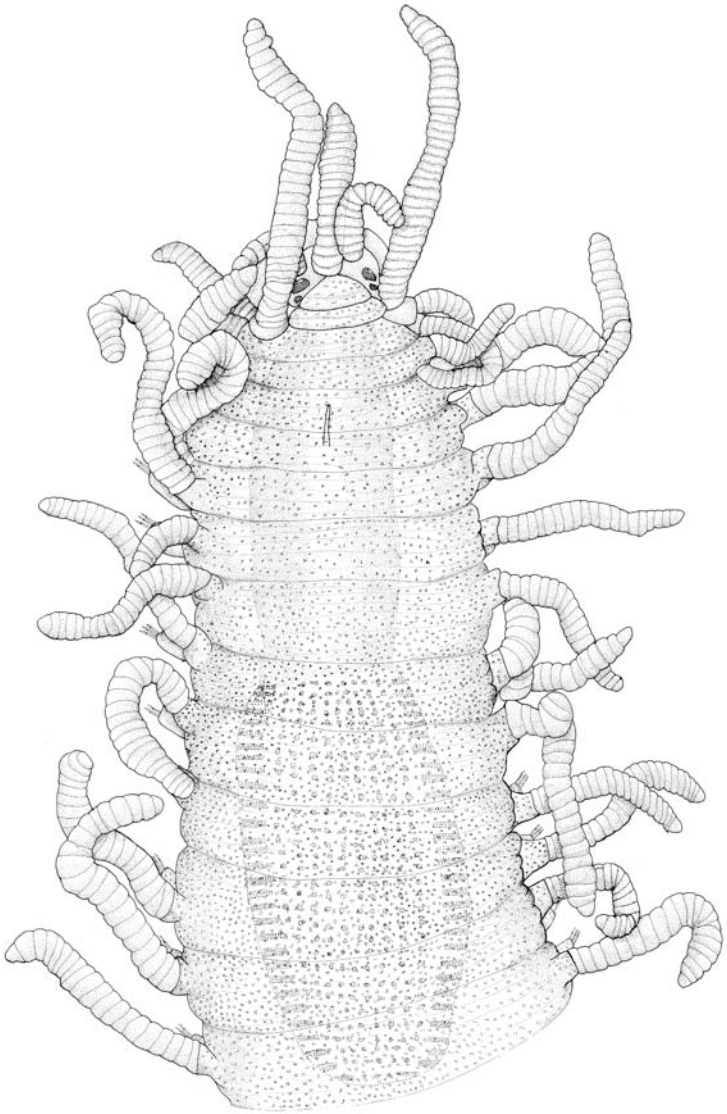
INTRODUCCIÓN



I. La Familia Syllidae Grube, 1850

II. La inferecia filogenética o Cladística

III. Estructura y motivación de la tesis

Los sílidos y esta tesis doctoral

Los sílidos son un grupo de anélidos poliquetos muy abundante aunque poco conocido a nivel divulgativo. La mayoría de la sociedad conoce el grupo de los anélidos porque, al menos, han estudiado su anatomía en las clases de secundaria. Podríamos decir que todo el mundo (aún siendo una generalización un poco vaga) ha visto o ha tenido algún contacto con una lombriz de tierra o incluso alguna sanguijuela. Es un poco menos común encontrar a alguien que conozca que muchos de los gusanos que se utilizan para pescar son poliquetos (mayoritariamente del género *Nereis*). Aunque en general, y de una manera pasiva, quien más quien menos, ha visto algún sabélido en un documental "de la 2". Sin embargo, "¿qué es un sílido?". Quizás sea esta la pregunta que más he oído durante los últimos años.

La palabra "sílido" proviene del nombre genérico *Syllis* que fue el que primero se utilizó para nombrar a unos animales similares a los *Nereis*. El término fue acuñado por Lamarck en 1818 pero las primeras descripciones de estos animales datan de 1771 por O.F. Müller. El nombre *Syllis* significa "gusano" en latín moderno (San Martín, 2003). Así parece que los sílidos no son más que eso, gusanos. Sin embargo, ser gusano, y en concreto ser sílido, es mucho más de lo que a un nivel divulgativo pueda parecer …

El iniciado en biología los conoce por su pequeño tamaño y por su abundancia en las aguas marinas. El estudiante de invertebrados se ha dejado sorprender por sus brillantes colores y su faringe evaginable. El investigador especialista en anélidos considera asombrosa la enorme variabilidad de tipos de reproducción presentes en el grupo (más de cuatro modos distintos que involucran cambios anatómicos sorprendentes). Pero, probablemente, el especialista en poliquetos, a pesar de disfrutar investigando sobre el grupo, no quiera tener que lidiar con sus abundantes y complicados problemas taxonómicos.

Los sílidos esconden aún la respuesta a muchas preguntas acerca de sus fascinantes modos de reproducción, su historia evolutiva y su distribución en la actualidad. Sin embargo, estos pequeños animales nos van permitiendo poco a poco saber algo más sobre su biología. Este ha sido el objetivo principal de esta tesis doctoral: adentrarnos en el mundo del sílido poliqueto, bucear en su intrincada taxonomía y resolver algunas incógnitas, viajar a su pasado y escribir algunos fragmentos de su historia, y en definitiva plantear nuevas preguntas, así como apuntar el modo de resolverlas.

I. La Familia Syllidae Grube, 1850

La familia Syllidae es una de las familias de poliquetos (Annelida) más numerosas, son un grupo altamente diversificado y se encuentra prácticamente en todos los hábitats marinos. Actualmente comprende más de 700 especies organizadas en más de 70 géneros (Pleijel, 2001, San Martín, 2003), sin embargo, existen aún muchas áreas geográficas sin estudiar por lo que el número de taxones nuevos para la ciencia continúa incrementándose. Se reconocen fácilmente como familia pero diferenciarlos a un nivel específico e incluso genérico es bastante difícil. La taxonomía del grupo es complicada, con múltiples excepciones y lagunas aún por resolver.

1. Hábitat y alimentación

Los sílidos son extraordinariamente abundantes en muestras litorales, aunque algo más escasos a grandes profundidades. La mayoría de los taxones viven en aguas templadas, especialmente en arrecifes de coral, pero el grupo es común prácticamente en todos los mares. Abundan entre las algas y rizomas de fanerógamas marinas, forman una parte importante de la criptofauna de substratos duros perforados por otros invertebrados, como rocas calizas, concreciones calcáreas y en sedimentos de todo tipo. Muchas especies son intersticiales en arenas (San Martín, 2003). Existen especies de sílidos asociadas a otros grupos de animales (esponjas, cnidarios, decápodos, equinodermos) (Martín y Britayev, 1998). Por ejemplo, las especies del complejo *Haplosyllis spongicola* y *Branchiosyllis oculata* viven dentro o sobre esponjas, se alimentan de ellas y, al ingerir el pigmento de la esponja, adquieren el mismo color que su hospedador (Fauchald y Jumars, 1979; Glasby, 2000). Muchos Autolytinae se alimentan y construyen tubos en hidroideos. La mayoría son sedimentívoros, aunque hay muchas especies herbívoras que se alimentan de algas, especies detritívoras, que se alimentan de detritus de origen vegetal y animal, así como especies omnívoras y carnívoras que se alimentan de diatomeas, algas, briozoos y una gran variedad de invertebrados (Fauchald y Jumars, 1979; Giangrande *et al.*, 2000; Pleijel, 2001). Los sílidos carnívoros podrían capturar sus presas utilizando su faringe eversible y el diente faríngeo, usando a continuación la potente musculatura del proventrículo para succionar el alimento (Fauchald y Jumars, 1979; Glasby, 2000). La llamativa coloración de algunos sílidos sugiere que podría tratarse de algún

tipo de aposematismo, pero no se ha realizado ningún estudio que corrobore esta hipótesis (Pleijel, 2001). Muchas especies, además, presentan coloraciones crípticas.

A pesar de su abundancia, los sílidos nunca son dominantes en biomasa: los individuos son normalmente cortos y delgados, a lo máximo con 10-20 mm de longitud y menos de 1 mm de diámetro. Muchas especies están dentro de la categoría de meiofauna, y otras muchas muestran un verdadero modo de vida intersticial (Westheide, 1984). Las adaptaciones al medio intersticial más documentadas en sílidos son las relacionadas con los cuidados parentales. Muchas especies intersticiales incuban los huevos (principalmente especies de Exogoninae) o son vivíparas (principalmente especies de Syllinae). El origen de estas especies intersticiales, con fenómenos reproductores propios de la meiofauna, podría ser explicado por procesos de paedomorfosis (Westheide, 1984; 1987).

2. Plan morfológico

El cuerpo es plano ventralmente y arqueado dorsalmente, o acintado en algún caso, con pocos o con numerosos segmentos, generalmente liso, pero en ocasiones puede llevar papilas epidérmicas, crestas longitudinales o bandas transversales de cilios. Las estructuras morfológicas que generalmente se encuentran en el cuerpo de los sílidos aparecen representadas en la figura 1 (Figs. 1A-C). El prostomio es redondeado o bien ovalado, con tres antenas (dos laterales y una central), que pueden ser lisas o articuladas. En la parte anterior del prostomio aparece un par de palpos cónicos que pueden estar reducidos, parcial o totalmente fusionados, y generalmente no articulados (Pleijel, 2001; San Martín, 2003). Generalmente tienen dos pares de ojos con lentes dispuestos en trapecio en el prostomio; y en posición anterior, puede aparecer un par adicional de ocelos o manchas oculares. Los órganos nucales se localizan en posición dorsal entre el prostomio y el peristomio. Pueden aparecer en forma de surco ciliado (en muchos géneros de Eusyllinae, Exogoninae y en Syllinae aunque con una excepción), o pueden aparecer como proyecciones nucales externas generalmente ciliadas conocidas como “nuchal lappets” o “nuchal eppaulettes” (en Autolytinae y en algunos Eusyllinae, en general). En algunas especies de Syllinae y Eusyllinae (géneros *Opisthosyllis* y *Odontosyllis*) aparece una proyección occipital (“occipital flap”) que cubre la parte posterior del prostomio. Rouse y Pleijel (2001) consideran que el peristomio es prácticamente invisible, probablemente reducido a los labios. Estos autores defienden que tradicionalmente se ha confundido el término peristomio con el segmento 1 aqueto. Sin embargo, nosotros

consideramos que los términos peristomio y cirros peristomiales para referirse al primer segmento aqueto, aunque probablemente erróneos, pueden seguir utilizándose dado que están muy afianzados en la taxonomía tradicional del grupo. El "peristomio" (o segmento 1) es aqueto y lleva dos pares de cirros ("cirros tentaculares"), uno o, excepcionalmente, ninguno. Por lo general aparece un par de cirros en posición más dorsal, normalmente de mayor longitud que el par más ventral.

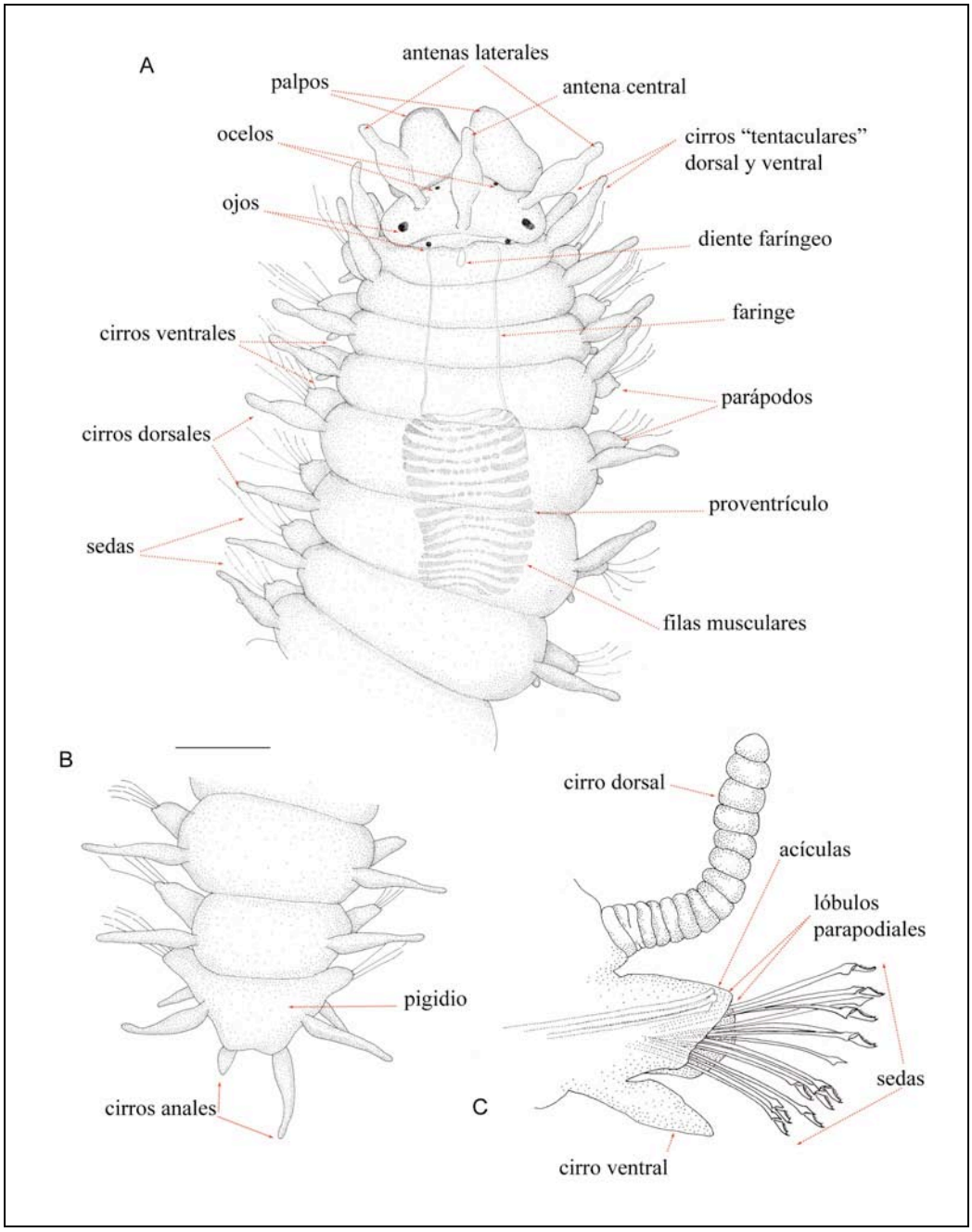


Figura 1. Terminología utilizada para las estructuras morfológicas de la familia Syllidae. A. Parte anterior de *Brania* sp. de Coiba (Pacífico de Panamá), vista dorsal; B. Parte posterior de *Brania* sp. de Coiba (Pacífico de Panamá), vista dorsal; C. Parápodo de *Syllis marugani* de Japón, vista lateral.

La parte anterior del tubo digestivo es visible por transparencia, y consta de una faringe más o menos larga y un proventrículo muscular y glandular. La faringe suele llevar en su abertura una, o excepcionalmente dos, coronas de papilas y, a veces, un anillo de cilios. La parte anterior de la faringe es eversible. Habitualmente aparece un **diente faríngeo** de consistencia quitinosa en la parte anterior y en posición interna y dorsal (en la mayoría de los Syllinae, Exogoninae y Eusyllinae), ocasionalmente retrasado o en la mitad posterior de la faringe (*Opisthosyllis* y *Opisthodonta*). En algunos géneros aparece en la parte anterior de la faringe un **arco ventral** de dentículos quitinosos (en algunos géneros de Eusyllinae). En otras ocasiones el anillo es completo, con dientes bien desarrollados, entonces se conoce como **trépano** (generalmente en Autolytinae). Sin embargo hay otros géneros (la mayoría de Eusyllinae o *incertae sedis*) que carecen de armadura faríngea.

La faringe puede ser recta o presentar varias vueltas (principalmente en Autolytinae). La faringe continúa en el **proventrículo**, una región muscularizada en el tubo digestivo que probablemente funciona como una bomba suctora, facilitando la adquisición del alimento (Fauchald y Jumars, 1979; Glasby, 2000). El proventrículo está constituido por un epitelio interno glandular y potentes fibras musculares dispuestas en posición radial (Haswell, 1921). La parte más externa de estas fibras es visible al microscopio óptico e incluso a la lupa binocular en forma de manchas circulares oscuras organizadas en filas. En el eje de cada una de esas fibras musculares hay numerosas inclusiones microcristalinas que contienen calcio y fósforo y que están relacionadas con el metabolismo del calcio (Glasby, 2000; San Martín, 2003). La característica más llamativa de los sílidos, junto con los fenómenos reproductivos, es la presencia del proventrículo. Su tamaño, forma y número de filas musculares son caracteres taxonómicos importantes para la identificación de las especies. La existencia de esta estructura tan característica y de fácil visualización por transparencia ha sido considerada como posible apomorfía del grupo (Glasby, 1993). A continuación del proventrículo, se encuentra una nueva especialización del tubo digestivo conocida como ventrículo, de paredes glandulares y escaso desarrollo muscular. Por detrás del ventrículo aparecen un par de ciegos gástricos laterales y, por último, el intestino es un tubo largo y delgado que recorre todo el resto de los segmentos.

Los podios son unirrámeos, manteniendo únicamente la rama ventral (o neuropodio) del típico parápodo birrámeo del grupo (condición primitiva en poliquetos, *s*. Rouse y Pleijel,

2001). La forma del parápodo suele ser cónica, soportado por una o varias neuroacículas, pudiendo presentar lóbulos pre y/o postsetales. La rama dorsal del parápodo (o notopodio) se desarrolla durante las etapas reproductivas en las especies que exhiben modificaciones para la reproducción (ver epigamia y esquizogamia en apartado 3). Estas especies, igualmente desarrollan notoacículas y notosedas. Los cirros dorsales, al igual que las antenas y los cirros tentaculares, pueden ser cortos, incluso papiliformes; o bien largos o muy largos; lisos (en general en Eusyllinae, Autolytinae y Exogoninae); o bien completa o incompletamente articulados (en la mayoría de los Syllinae y algunos Eusyllinae). En algunos géneros (p. e. *Sphaerosyllis*) faltan los cirros dorsales del segundo setígero. En general, parece que los cirros dorsales muestran un patrón de alternancia tanto en longitud como en orientación, aunque no se ha podido constatar en la mayoría de las especies ya que es necesario estudiar material en vivo para percibir las diferencias en la orientación de los cirros. Los parápodos normalmente carecen de branquias, a excepción de algunas especies del género *Branchiosyllis*.

Las neurosedas son generalmente compuestas, con artejos largos o cortos, pero mango y artejo pueden estar fusionados para formar gruesas sedas simples (p. e. en *Haplosyllis* y en algunas especies de *Syllis*) (Paola *et al*., 2006). Hay además una seda simple capilar dorsal y otra ventral que pueden aparecer desde los primeros segmentos, o solamente en podios posteriores. Cuando sólo se encuentran en segmentos posteriores, las sedas simples dorsales suelen aparecer algunos segmentos por delante de las simples ventrales. Los cirros ventrales son cortos, digitiformes, en ocasiones ausentes (en Autolytinae) aunque podrían estar fusionados al parápodo (Nygren, 1999; San Martín, 2003). El pigidio tiene dos cirros anales, similares a los dorsales y, en ocasiones, un corto apéndice impar no articulado. Una descripción mucho más detallada de la anatomía general de los sílidos puede encontrarse en San Martín (2003).

La segmentación del cuerpo es homónoma, aunque detalles como la forma de las sedas y el número de acículas por parápodo podrían sugerir que existen distintas “regiones”. Las diferencias entre estas “regiones” son graduales, por lo que los límites entre ellas no están nunca claros; además su extensión varía mucho con el tamaño del animal. En general, hay una primera “región”, inmediatamente posterior al prostomio y peristomio, con parápodos provistos de sedas compuestas de artejos relativamente largos, varias acículas por parápodo y, por lo general, sin sedas simples; luego hay una “región” intermedia, con menor número de acículas por parápodo y sedas de artejos más cortos y anchos; y por último, podríamos

considerar una “región” posterior que llevaría una sola acícula por parápodo, más gruesa que las anteriores, sedas simples dorsal y ventral, y menos sedas compuestas, más gruesas y con artejos más cortos y anchos. Estas “regiones” varían mucho de unos géneros a otros y hay multitud de excepciones. Sin embargo, las disminuciones del número de sedas por parápodo, y de la longitud de los artejos en sentido antero-posterior, a la vez que aumenta la anchura de los artejos, así como la disminución del número de acículas en sentido antero-posterior y aparición de sedas simples capilares en la última parte del cuerpo parecen ser una norma general dentro de los Sílidos (San Martín, 2003).

Los sílidos muestran gran capacidad de regeneración de los segmentos perdidos. Por lo general, son capaces de regenerar los segmentos posteriores tras la formación y liberación del estolón (ver esquizogamia), siempre que la ruptura se haya producido por detrás del comienzo del intestino (Okada, 1929; 1938; Glasby, 2000). Muchas especies son también capaces de regenerar los segmentos anteriores, incluyendo la región faríngea y el prostomio (Okada, 1929).

3. Reproducción

Existen numerosos trabajos que tratan sobre la biología reproductiva de los sílidos, entre los que destacan los trabajos de Malaquin (1893), Potts (1911), Okada (1937), Durchom (1959), Durchom y Wissocq (1964), Gidholm (1965), Garwood (1991), Franke (1999) y Nygren (1999). Los sílidos presentan una enorme diversidad de fenómenos reproductivos. Se pueden reproducir asexual y sexualmente. En la reproducción sexual, suelen aparecer sexos separados aunque también se encuentran especies hermafroditas en las cuatro subfamilias. Hay dos procesos reproductivos principales: la epigamia, en la que todo el animal se involucra en la reproducción, y la esquizogamia, en la que el progenitor desarrolla estolones que serán las unidades reproductivas (Fig. 2A).

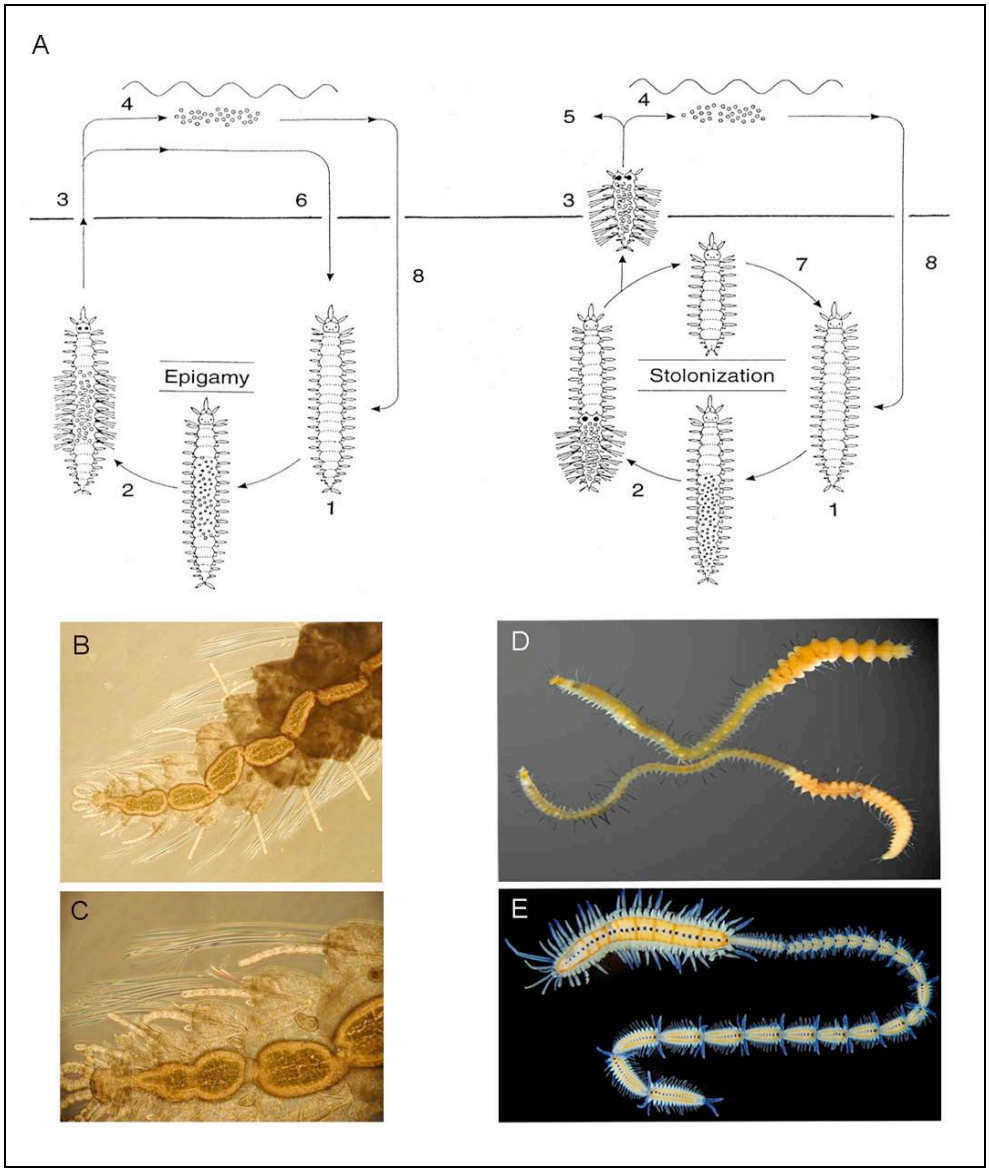


Figura 2. Distintos modos de reproducción en Syllidae. A. Epigamia y esquizogamia (tomado de Franke, 1999), 1: forma átoca, 2: maduración sexual y transformación a la fase epítoca, 3: liberación de los gametos, 4: fecundación, 5: muerte del estolón, 6: vuelta a la vida bentónica, 7: regeneración de la parte posterior, 8: desarrollo larvario y del juvenil; B, C. Parte posterior de un ejemplar epigámico; detalle de sedas natatorias (fotos por Matthew R. Lee); D. Dos Syllinae desarrollando cada uno de ellos un estolón en su parte posterior (escisiparidad posterior) (foto por Leslie Harris); E. Ejemplar de *Myrianida pachycera* desarrollando una cadena de estolones (gemmiparidad) (foto por Leslie Harris).

La **epigamia** se ha citado para los géneros de Eusyllinae, Exogoninae y *Epigamia* en Autolytinae. Consiste en cambios importantes en la anatomía y fisiología que experimenta el individuo en su madurez sexual. Los ojos aumentan de tamaño y las antenas aumentan su longitud; en la mitad o 2/3 posteriores del cuerpo los parápodos adquieren un notopodio formado por una notoacícula y un haz de notosedas simples, capilares, muy largas

consideradas sedas natatorias (Figs. 2B, C); las glándulas genitales se desarrollan en los segmentos modificados del cuerpo, y éstos se cargan de espermatozoides o de óvulos, de manera que los segmentos afectados se engruesan mucho y adquieren una coloración distinta al resto del cuerpo, más oscura. Junto con estos cambios estructurales hay cambios en el comportamiento, ya que los ejemplares se vuelven más activos y nadadores, pudiendo formar grandes enjambres de individuos nectónicos reproductores. A los individuos modificados se les denomina también formas **epítoca** o **epígama**, y a los no modificados formas **átoca** o **ágama** (San Martín, 2003). Algunos sílidos epigámicos (*Streptosyllis websteri* y muchos Exogoninae) pueden sobrevivir tras los procesos reproductivos, sin embargo, otras especies, como *Streptosyllis verrilli* mueren tras la reproducción (Franke, 1999; Glasby, 2000; Pleijel, 2001). Los procesos de bioluminiscencia parecen ser comunes en las hembras de distintas especies epigámicas de Eusyllinae (p. e. *Odontosyllis*) (Fischer y Fischer, 1995; Glasby, 2000; Pleijel, 2001). Estos procesos podrían estar relacionados con la atracción de los machos.

En la subfamila Exogoninae existen además dos tipos de incubación: incubación de los huevos en posición dorsal y sujetos por las notosedas (Fig. 3C), o incubación ventral de los huevos unidos al nefridioporo y posterior desarrollo de los juveniles, también unidos al cuerpo de la madre (Fig. 3D) (Mastrodonato *et al.*, 2003). Algunos autores han sugerido que estos dos tipos distintos de incubación pueden indicar la existencia de dos líneas evolutivas diferentes dentro de los Exogoninae (San Martín, 2003, 2005).

La **esquizogamia** se da tanto en la subfamilia Syllinae como en la Autolytinae. Este tipo de reproducción consiste en la separación de una porción del individuo que adquiere movimiento propio y vida independiente. Dicha porción del cuerpo, o **estolón**, lleva los gametos, carece de tubo digestivo, no se alimenta, y muere una vez expulsados los productos sexuales. Este estolón lleva sedas natatorias en la mayoría de sus parápodos (Figs. 3A, B). Una vez maduro, se desprende del individuo parental y migra a la superficie o queda cerca del fondo marino, para reproducirse. La esquizogamia, a pesar de consistir en un proceso tan concreto como es la formación de estolones, se manifiesta de forma muy diferente en cada una de las subfamilias (San Martín, 2003). Existen dos tipos de esquizogamia, **gemmiparidad**, cuando se desarrolla una cadena de estolones (Fig. E), y **escisiparidad**, cuando únicamente se desarrolla un único estolón (Fig. 2D). La escisiparidad puede a su vez dividirse en dos tipos diferentes: **escisiparidad anterior**, cuando el estolón se desarrolla antes del setígero 13, o **escisiparidad posterior**, cuando el estolón aparece por detrás del setígero 13) (Nygren &

Sundberg, 2003). La escisiparidad posterior ocurre en Syllinae, mientras que la gemmiparidad y ambas escisiparidades tiene lugar en Autolytinae y la gemmiparidad concretamente en el género *Myrianida*. Estapé y San Martín (1991) estudiaron cinco tipos distintos de estolones en Syllinae: acéfalos, ácero o *Tetraglene*, dícero o *Chaetosyllis*, tetrácero y pentácero o *Ioda*. Posteriormente San Martín *et al*. (1997) describieron un sexto tipo de estolón en el género *Haplosyllides*. Estos tipos diferentes de estolones se diferencian principalmente en la estructura y apéndices de la parte anterior. No existe dimorfismo sexual ni regionalización en los estolones de Syllinae. Sin embargo, en Autolytinae, los estolones se caracterizan por presentar regionalización (fig. 3A) y un dimorfismo sexual muy marcado. El estolón masculino se denomina *Polybostrichus* y el femenino *Sacconereis*. En estas especies, el estolón hembra emite una feromona sexual que induce al estolón macho a "bailar" en círculo a su alrededor a medida que expulsa el esperma que va fecundando los huevos, en ocasiones los embriones se desarrollan en una bolsa de incubación derivada del saco ovígero (Gidholm, 1965; Qian y Chia, 1989; Glasby, 2000, San Martín, 2003) (Figs. 3E, F).

El proceso de la estolonización parece estar controlado por un sistema endocrino conectado al proventrículo, al menos en algunas especies de Syllinae (Durchon, 1957; Franke, 1980, 1983; Heacox y Schroeder, 1982). Tras producirse la estolonización, las glándulas del proventrículo segregan hormonas inhibidoras que impiden el desarrollo de un nuevo estolón y activa la regeneración de los segmentos que se han perdido; sin embargo, la disminución de estas hormonas provoca la maduración sexual y la formación del estolón. Según Franke (1986) en sus experimentos con *S. prolifera*, el nivel de la hormona inhibidora decrece periódicamente durante los meses de verano, ya que la periodicidad de los niveles de esa hormona se corresponde con los ciclos lunares del verano. Schiedges (1979) demostró que el fotoperiodo diurno es la causa externa de estolonización en algunas especies de *Myrianida*. Los estolones femeninos nadan hacia la luz y se quedan cerca de la superficie, mientras que los masculinos son atraídos mediante una feromona sexual femenina. En algunas especies se ha podido comprobar que cada ejemplar puede cambiar de sexo de una estolonización a otra, p. e. *Syllis amica* (Durchon,1951). Una información más extensa sobre los procesos reproductivos aparece recogida en San Martín (2003).

Un patrón de estolonización diferente se da en la especie *Syllis ramosa* y *Syllis* sp. Estas especies viven en el interior de esponjas y presentan ramificaciones de su cuerpo que introducen en los distintos canales internos de la esponja. Las ramificaciones presentan múltiples estolones tanto femeninos como masculinos (Mc Intosh, 1879; observaciones

personales en *S. ramosa*; Glasby, com. pers.) (Fig. 3G-I). También se ha descrito la formación de varios estolones laterales, por el desarrollo de yemas en la parte posterior del cuerpo como en el género *Trypanosyllis* (Garwood, 1991; San Martín, 2003) (Fig. 3J).

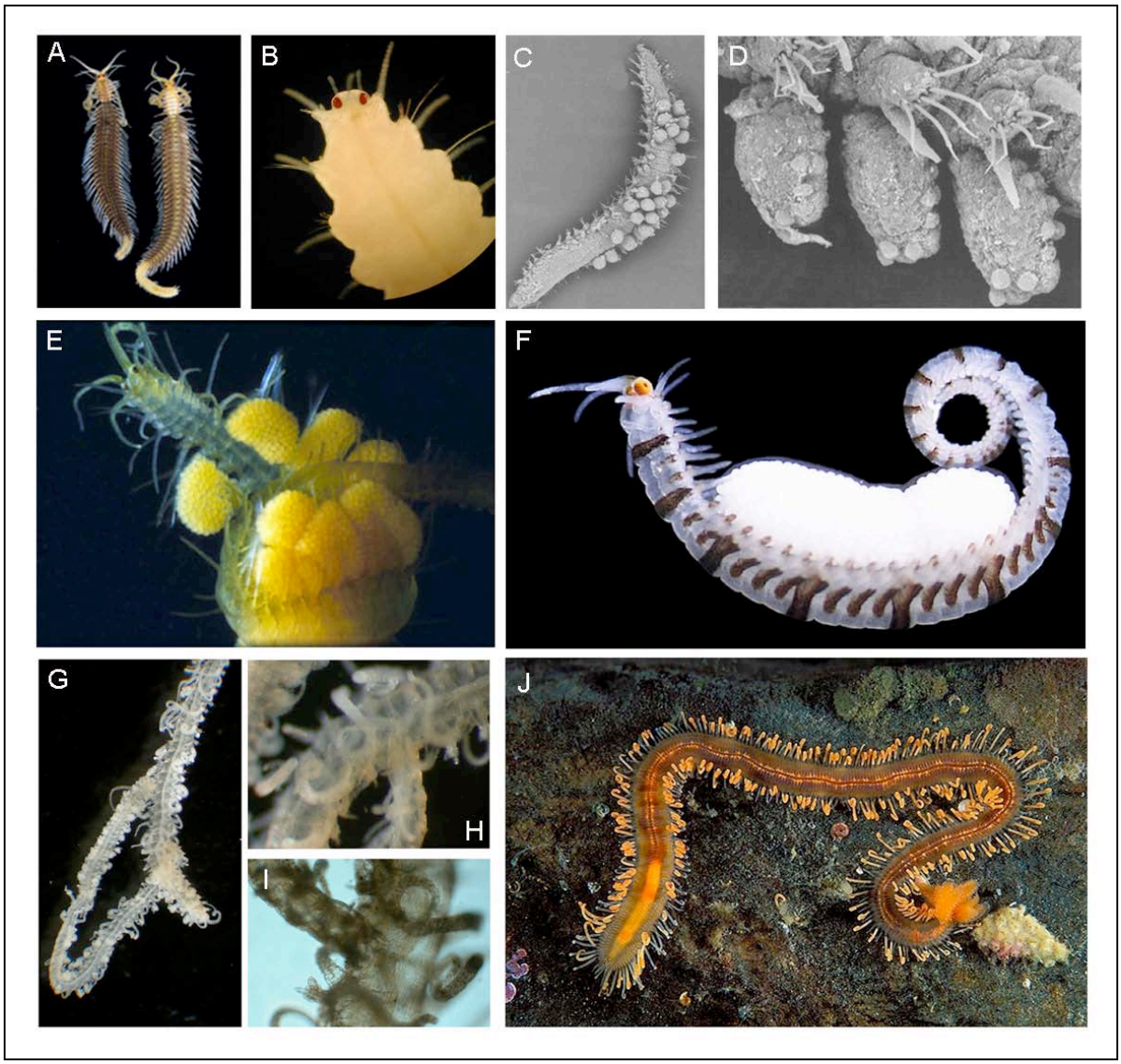


Figura 3. Distintos sílidos durante el proceso reproductivo. A. Estolones de Autolytinae (foto por Leslie Harris); B. Estolón de Syllinae (foto por Matthew R. Lee); C. Exogoninae con incubación dorsal (San Martín, 2003); D. Exogoninae con incubación ventral y desarrollo de juveniles (San Martín, 2003); E, F. Autolytinae incubando en sacos ventrales (fotos por Alexandra A. Bely y Leslie Harris); G-I. Detalles de las ramificaciones en el cuerpo de *Syllis ramosa*; H. *Trypanosyllis* con un racimo de estolones en su parte posterior (foto por E. Nishi).

Por lo general, los sílidos son animales de sexos separados, aunque hay casos citados de **hermafroditismo** simultáneo en algunos Exogoninae y hermafroditismo secuencial en algunos Exogoninae y Syllinae (Westheide, 1990; Franke, 1999). Se han descrito también

casos de **viviparismo** (Goodrich, 1900; Webster y Benedict, 1884; Pocklington y Hutchenson, 1977; San Martín, 1984, etc.) de manera puntual en algunas especies de Syllinae y Exogoninae (géneros *Syllis*, *Paraexogone*, *Dentatisyllis*). Estas especies desarrollan juveniles en el interior de su cuerpo que se alimentan del líquido celomático a través de su tubo digestivo aún en formación o de materia orgánica disuelta a través de la epidermis (Ding, Licher & Westheide, 1998; Glasby, 2000).

La fase larvaria (que puede estar ausente en las especies con incubación) es más corta que en otras familias de poliquetos (Glasby, 2000). Esta larva desarrolla bandas ciliares en estadios previos a la fase trocófora. En muchas especies (a excepción de Exogoninae), además presenta un penacho de espinas en posición apical. El desarrollo larvario ha sido descrito para algunas especies de *Sylis*, *Epigamia* y *Myrianida* (Pleijel & Rouse, 2006), aunque la información de la que disponemos acerca de los ciclos de vida de los sílidos es aún muy escasa (Glasby, 2000).

4. Taxonomía

Aunque existen numerosos trabajos sobre la familia Syllidae, ningún estudio hasta la fecha ha abordado la sistemática de los sílidos en su conjunto. Ni siquiera el número de géneros dentro de la familia parece estar claro. Así mismo, existen numerosos casos dudosos y múltiples sinonimias que dificultan aún más la organización del grupo. Muchas especies no muestran suficientes caracteres diagnósticos en la descripción, por lo que una revisión y una redescripción apropiada son totalmente necesarias. Esta tesis pretende solventar estas carencias haciendo contribuciones al conocimiento taxonómico y sistemático de la familia Syllidae, investigando en las relaciones entre los taxones, para concluir con una clasificación actualizada del grupo.

El primer autor en dividir la familia fue Langerhans (1879) al proponer tres tribus dentro de Syllidae: *Syllideae* Grube, 1850, *Exogoneae* Langerhans, 1879 y *Autolyteae* Langerhans, 1879. Posteriormente, Malaquin (1893) añadió la tribu *Eusylleae*. El primero en dar categoría de subfamilias fue Fauvel (1923), seguido por Rioja (1925). La clasificación actual divide la familia en cuatro subfamilias: Syllinae Grube, 1850; Exogoninae Langerhans, 1879;

Eusyllinae Malaquin, 1893; y Autolytinae Langerhans, 1879 (Fauchald, 1977; San Martín, 2003).

Los **Autolytinae** se reconocen por la presencia de palpos reducidos y fusionados, órganos nucales externos o "nuchal epaulettes", una faringe larga y sinuosa, cirros ventrales ausentes, cirros dorsales lisos y reproducción por esquizogamia. Los **Exogoninae** se distinguen por su pequeño tamaño, grandes palpos que pueden estar parcial o totalmente fusionados, órganos nucales poco visibles, faringe recta, cirros dorsales cortos y lisos, presencia de cirros ventrales, ausencia de bandas ciliares segmentarias en las larvas y reproducción por epigamia con incubación dorsal y ventral. Los **Syllinae** se reconocen por tener palpos basalmente fusionados, órganos nucales en forma de fosetas ciliadas, antenas, cirros tentaculares y dorsales articulados, presencia de cirros ventrales, bandas ciliares segmentarias en las larvas y reproducción por esquizogamia. Por último, los **Eusyllinae**, aunque no tienen unos caracteres morfológicos uniformes, habitualmente se han distinguido por tener palpos fusionados basalmente, órganos nucales en forma de fosetas ciliadas o externos en forma de "nuchal epaulettes", antenas, cirros tentaculares y dorsales lisos o irregularmente articulados, presencia de cirros ventrales, bandas ciliares segmentarias en las larvas y reproducción por epigamia.

Actualmente, esta clasificación se considera insatisfactoria porque no está fundamentada en la sistemática filogenética y parece estar en uso principalmente por razones prácticas (Fauchald, 1977; Glasby, 2000; San Martín y López, 2003; San Martín, 2003). El carácter monofilético de esta agrupación en subfamilias presenta controversia, ya que cada vez es más evidente que muchas especies y géneros (e.g. algunas especies de *Pionosyllis*, *Parapionosyllis*, *Syllides*, *Haplosyllides*) no pueden ser asignados, exclusivamente por caracteres morfológicos, a una de las subfamilias (San Martín y Estapé, 1993; Jiménez *et al.*, 1994; San Martín, 2003). Algunos autores sugieren que el tipo de reproducción es de decisiva importancia en la definición de grupos monofiléticos (San Martín, 1984; Garwood, 1991).

Los caracteres más importantes para el reconocimiento de géneros de la familia son: 1) forma del cuerpo: subcilíndrica o acintada.; 2) número de antenas; 3) estado de los palpos: libres, parcialmente o completamente fusionados; 4) número de pares de cirros tentaculares; 5) presencia o ausencia de cirros ventrales; 6) tamaño y disposición de antenas, cirros tentaculares y cirros dorsales; 7) armadura de la faringe y tamaño relativo; 8) forma de las sedas; y 9) tamaño relativo del proventrículo y número de filas musculares.

5. Filogenia

La familia Syllidae forma parte del grupo monofilético Phyllodocida (Rouse y Fauchald, 1997; Rouse y Pleijel, 2001) (Fig 4A). El clado Phyllodocida contiene un elevado número de familias de poliquetos, pero las relaciones entre estas familias no están totalmente claras y varían dependiendo del análisis filogenético que se considere (Pleijel, 2001). La familia Syllidae podría ser el grupo hermano de los Phyllodocida, según Rouse y Fauchald (1997); sin embargo, para Glasby (1993) y Pleijel y Dahlgren (1998), Phyllodocida podría contener dos grupos monofiléticos internos: Aphroditiformia and Nereidiformia, aunque algunas familias de Phyllodocida no se posicionan claramente en ninguno de los dos clados. Según estos autores, Nereidiformia contendría a la familia Syllidae junto con Chrysopetalidae, Hesionidae, Nautilienidae, Nereididae and Pilargidae (Fig. 4B).

La sistemática de poliquetos, en general, y del clado Phyllodocida, en particular, se ha obtenido a partir de análisis filogenéticos basados exclusivamente en datos morfológicos. Actualmente, hay muy pocos estudios sobre la filogenia de las familias de Phyllodocida que incluyan datos moleculares (Dahlgren *et al.*, 2000; Nygren and Sundberg, 2003; Nygren, 2004; Nygren *et al.*, 2005; Wicklund *et al.*, 2005; Worsae *et al.*, 2005). Algunos de los análisis moleculares más recientes sobre la filogenia de poliquetos en general no apoyan la monofilia de Phyllodocida (Brown *et al.*,1999; Bleidorn, 2003a; Hall *et al.*, 2004; Worsae *et al.*, 2005). Sin embargo, muchos autores han llamado la atención sobre la escasa representación de poliquetos, en particular de Phyllodocida en las bases de datos moleculares. Por lo tanto, existe una creciente necesidad de incrementar la muestra de taxones para los que disponemos de datos moleculares que nos permitan finalmente, y junto con los datos morfológicos, elaborar una hipótesis más robusta sobre la filogenia de los anélidos (Struck, 2002, 2005; Bleidorn, 2003a,b; Hall *et al.*, 2004).

Worsaae *et al.*, 2005 en su análisis combinado con datos morfológicos y moleculares mostraron a la especie del sílido *Eusyllis blomstrandi* como un taxón cercano a *Nereis pelagica* (Nereidae). Wiklund *et al.* (2005) encontraron que *E. blomstrandi* se colocaba dentro de un grupo monofilético junto con *Dysponetus* (Chrysopetalidae) y representantes de Nereidae. En el análisis molecular llevado a cabo por Hall *et al.* (2004), el sílido *Proceraea cornuta* aparece como el grupo hermano de un clado que contiene a Orbinidae y Questidae (Scolecida), no relacionado con el resto de los Phyllodocida. Rousset *et al.* (2007)

encontraron a los sílidos como grupo hermano de los sabeláridos y polinoidos. Estos resultados son poco concluyentes y muestran el elevado nivel de desconocimiento sobre el tema.

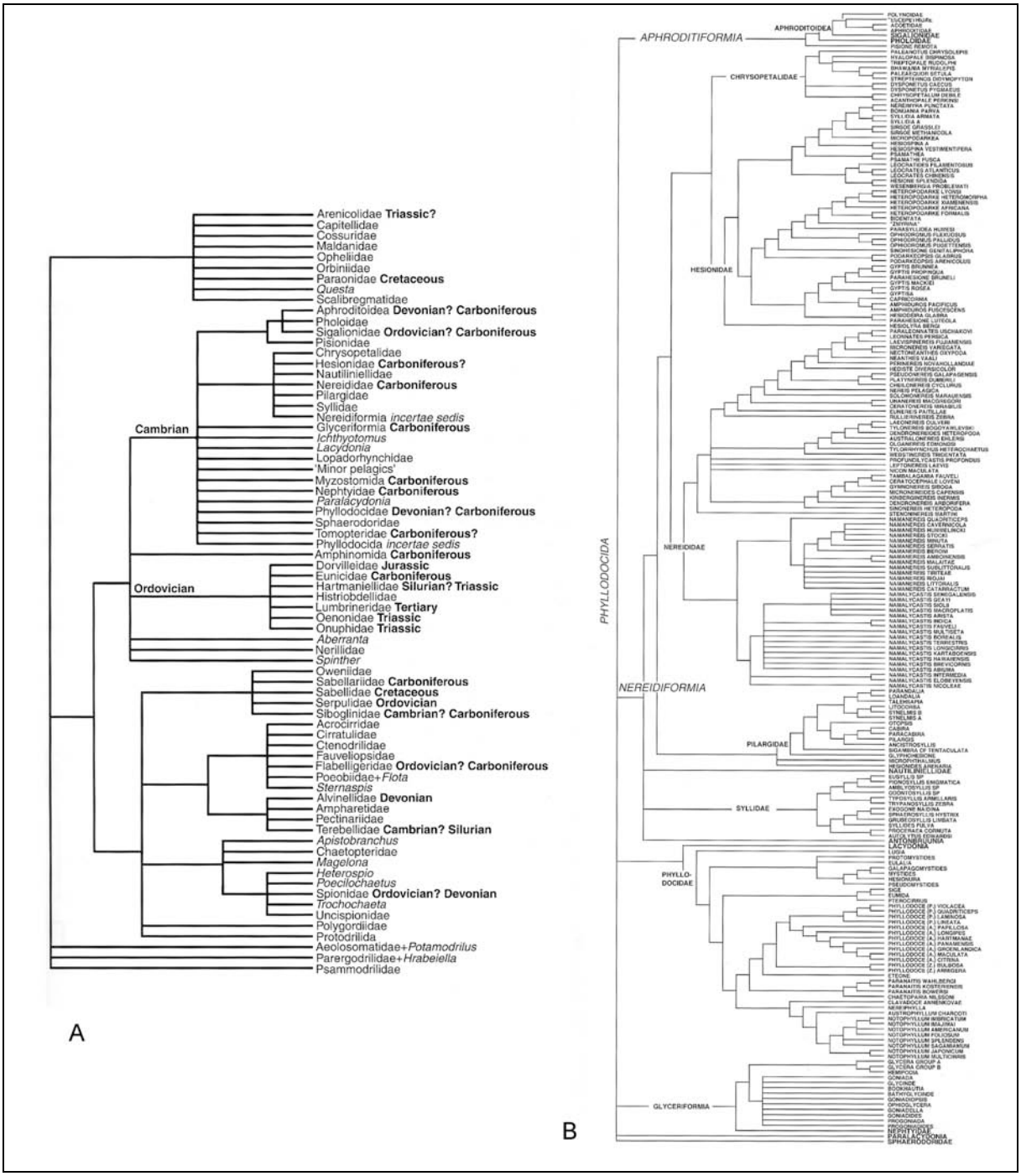


Figura 4. A. Organización sistematica de los poliquetos basada en el análisis cladístico de Rouse y Fauchald (1997); B. E clado Phyllodocida extraído del "metatree" de los poliquetos que reúne distintas hipótesis filogenéticas sobre los distintos grupo de poliquetos. (Ambas figuras tomadas de Rouse y Pleijel, 2001).

Hasta la presente tesis doctoral, había sólo cuatro estudios cladísticos que atienden a las relaciones filogenéticas dentro de la familia Syllidae (Licher, 1999; Nygren, 1999; Nygren y Sundberg, 2003 y Nygren, 2004).

Licher (1999) realizó una revisión del género *Typosyllis* considerado en esta tesis doctoral y por otros autores como sinónimo de *Syllis* (San Martín, 1984, 2003). Para Licher (1999) *Typosyllis* carece de sedas simples, mientras que *Syllis* si las presenta. Sin embargo, como ya se ha mencionado anteriormente, las sedas simples parecen ser el resultado de un proceso de fusión entre el mango y el artejo de sedas compuestas. Además, este proceso aparece de manera independiente en varios géneros como una adaptación a la vida en asociación con otros organismos (como esponjas o corales). Por estas razones, no consideramos justificado el mantener *Syllis* y *Typosyllis* como dos géneros diferentes. Licher (1999) propuso una hipótesis, aunque no basada en métodos cladísticos, sobre las relaciones evolutivas entre las subfamilias y algunos géneros (Fig. 5A). En esta hipótesis, *Syllides*, *Astreptosyllis*, *Streptosyllis* and *Streptospinigera* aparecieron como el grupo hermano del resto de los sílidos que aparecían organizados en las clásicas subfamilias, de las que Eusyllinae podía ser un grupo parafilético, y Autolytinae y Syllinae podían mantener una relación cercana de parentesco. El mismo autor organizó las especies de *Syllis* sin sedas simples ("*Typosyllis*") en 18 complejos en función de sus similitudes morfológicas (principalmente en la forma de las sedas) y realizó un análisis cladístico incluyendo dichos complejos de especies, encontrando que se podían organizar en tres grandes clados (el grupo *cornuta*, el grupo *prolifera* y el grupo *armillaris*) (Fig. 5B).

Nygren (1999) estudió la evolución de los procesos reproductivos en sílidos, utilizando 44 caracteres morfológicos y 12 representantes de la familia. Este estudio pretendía comprobar la monofilia de las cuatro subfamilias y descifrar las relaciones evolutivas entre los distintos tipos de reproducción en la familia. Los resultados, aunque limitados por los escasos taxones de sílidos incluidos en el análisis, indicaron que tres de las subfamilias podían ser monofiléticas (Syllinae, Autolytinae y Exogoninae), y que los sílidos que incuban huevos podían formar parte del mismo grupo monofilético. Sin embargo, este estudio no pudo resolver las preguntas acerca de cuál de los procesos reproductivos (epigamia o esquizogamia) era el ancestral y cuál el derivado (Fig. 6A).

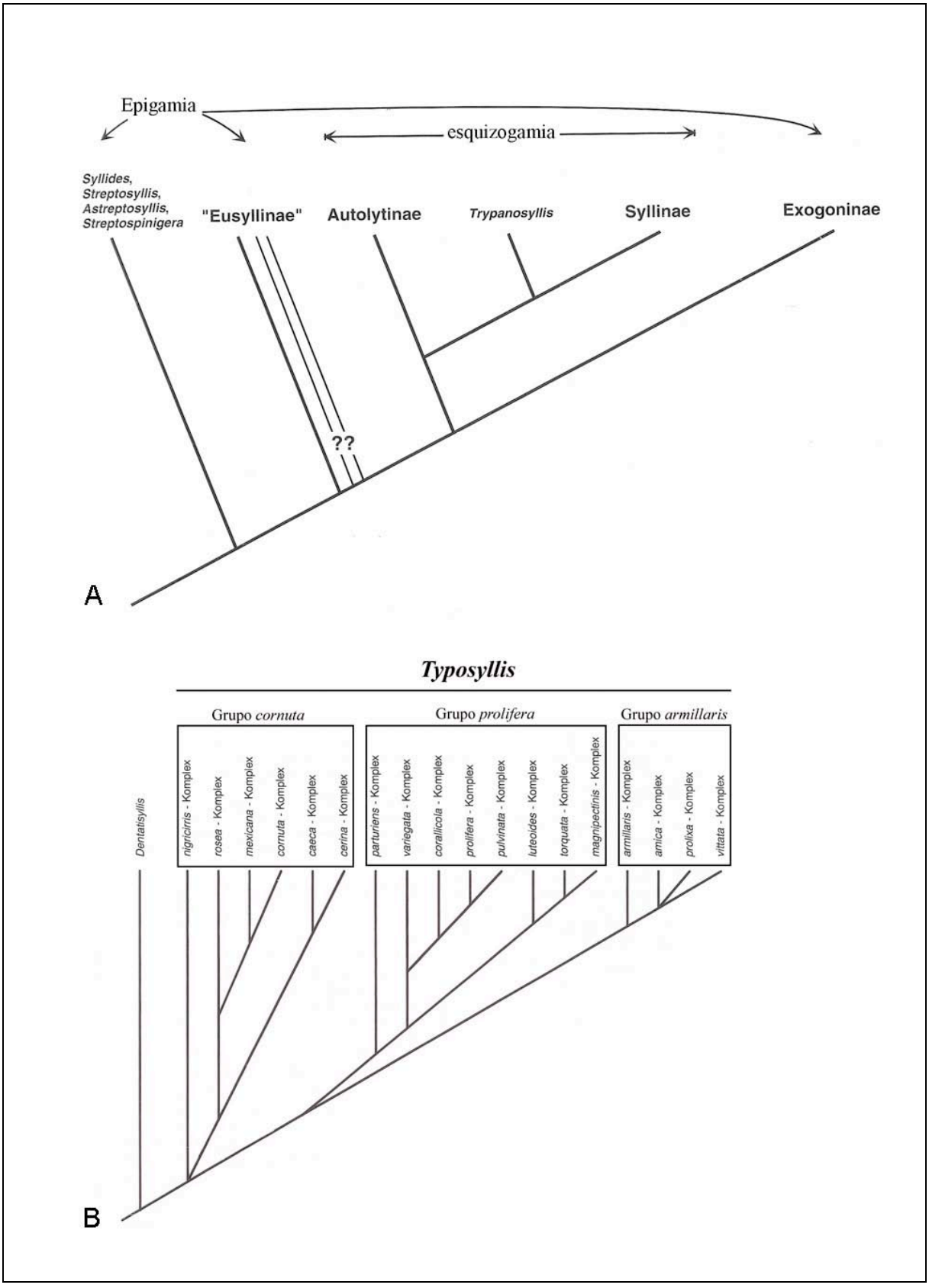


Figura 5. A. Hipótesis sobre las relaciones evolutivas entre las familias de Syllidae; B. Consenso estricto del análisis filogenético llevado a cabo con las especies de *Syllis* de sedas compuestas ("*Typosyllis*" *s*. Licher, 1999). (Ambas figuras tomadas de Licher,1999).

Posteriormente, Nygren y Sundberg (2003) reconsideraron la evolución de los procesos reproductivos en la subfamilia Autolytinae utilizando caracteres moleculares. Estos autores utilizaron las secuencias de ADN del gen nuclear 18S y el gen mitocondrial 18S para 31 representantes del grupo y 12 grupos externos, entre los que incluyeron sílidos de otras subfamilias y representantes de familias de poliquetos relacionadas con los sílidos. Los dos genes fueron analizados separadamente y en un análisis combinado utilizando parsimonia, máxima verosimilitud y análisis bayesiano (ver apartado de Cladística en la Introducción). Independientemente del método utilizado, los resultados siempre coincidieron en soportar la división de Autolytinae en tres grandes grupos: uno con las especies epigámicas, otro con las especies esquizogámicas con escisiparidad posterior y gemmiparidad y, por último, un tercer grupo incluyendo las especies esquizogámicas con escisiparidad anterior (Fig. 6B). Las relaciones entre estos tres grupos no se pudieron resolver. Los análisis llevados a cabo con parsimonia y máxima verosimilitud mostraron la epigamia como el estado plesiomórfico en Syllidae y la esquizogamia como el estado derivado que apareció de manera independiente en Autolytinae y en Syllinae.

Por último, Nygren (2004) realizó una revisión de la subfamilia Autolytinae combinando datos morfológicos y moleculares. En este análisis se utilizaron 51 caracteres morfológicos para 76 taxones y las secuencias de los genes 18S y 16S de 31 taxones de autolytinae, junto con 12 representantes del resto de las subfamilias. Se realizaron dos análisis diferentes, uno incluyendo únicamente los datos morfológicos y otro incorporando el análisis combinado de la información morfológica junto con la molecular. El consenso estricto del análisis combinado se utilizó para elaborar una nueva propuesta de clasificación para la subfamilia Autolytinae (Fig. 7). Dentro de Autolytinae, aparecieron tres grandes grupos bien soportados: Procerini, Autolytini y *Epigamia*. En Autolytinae, el modo reproductivo ancestral podría ser la epigamia, mientras que la esquizogamia podría considerarse como estado derivado.

La clasificación propuesta en este último trabajo para Autolytinae (Nygren, 2004) es la que se ha utilizado en esta tesis doctoral.

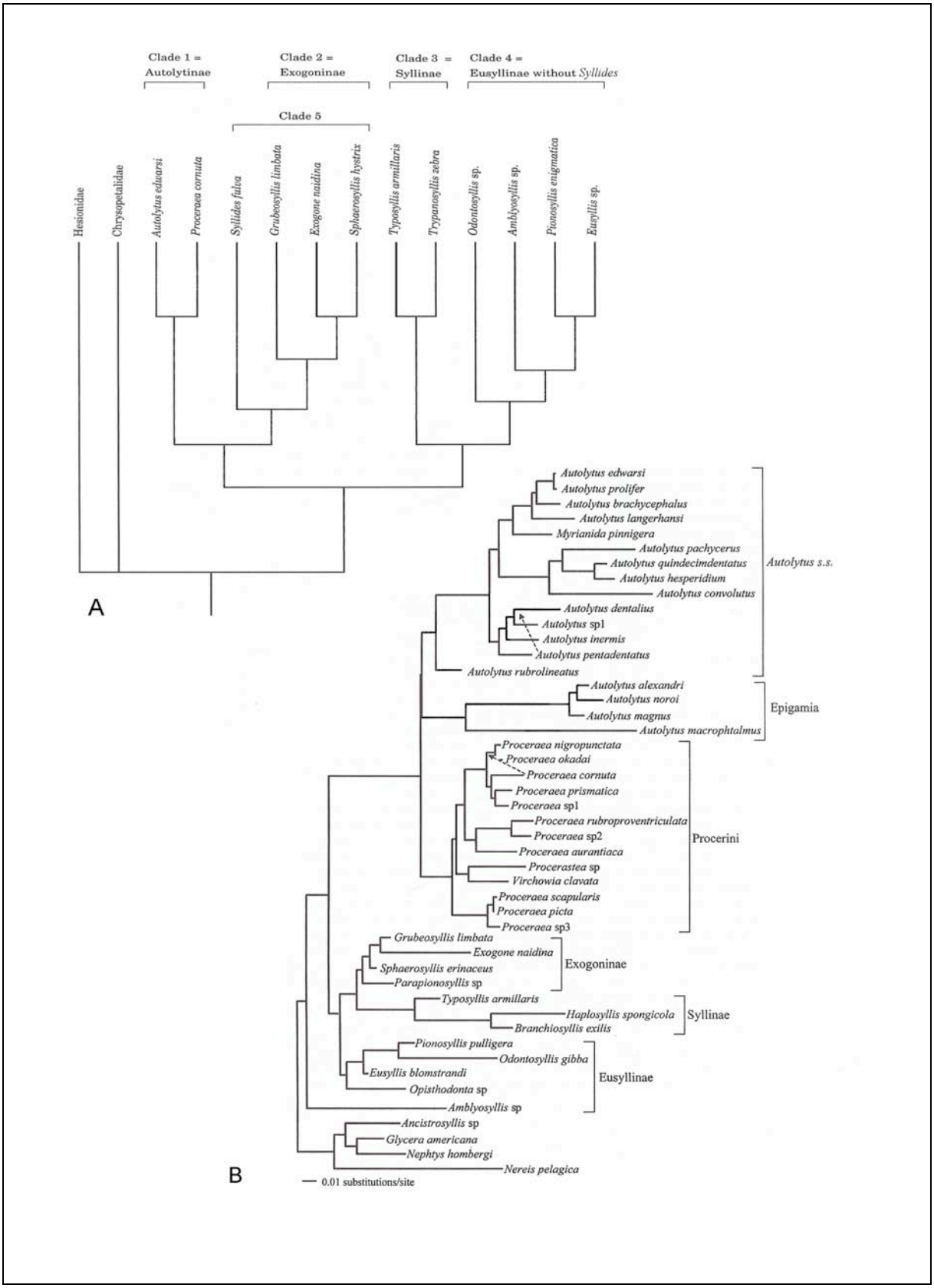


Figura 6. A. Árbol más parsimonioso obtenido en el análisis morfológico de Nygren (1999); B. Árbol de máxima verosimilitud obtenido del análisis combinado de datos moleculares llevado a cabo por Nygren y Sundberg (2003). (Modificadas de Nygren, 1999 y Nygren y Sundberg, 2003, respectivamente).

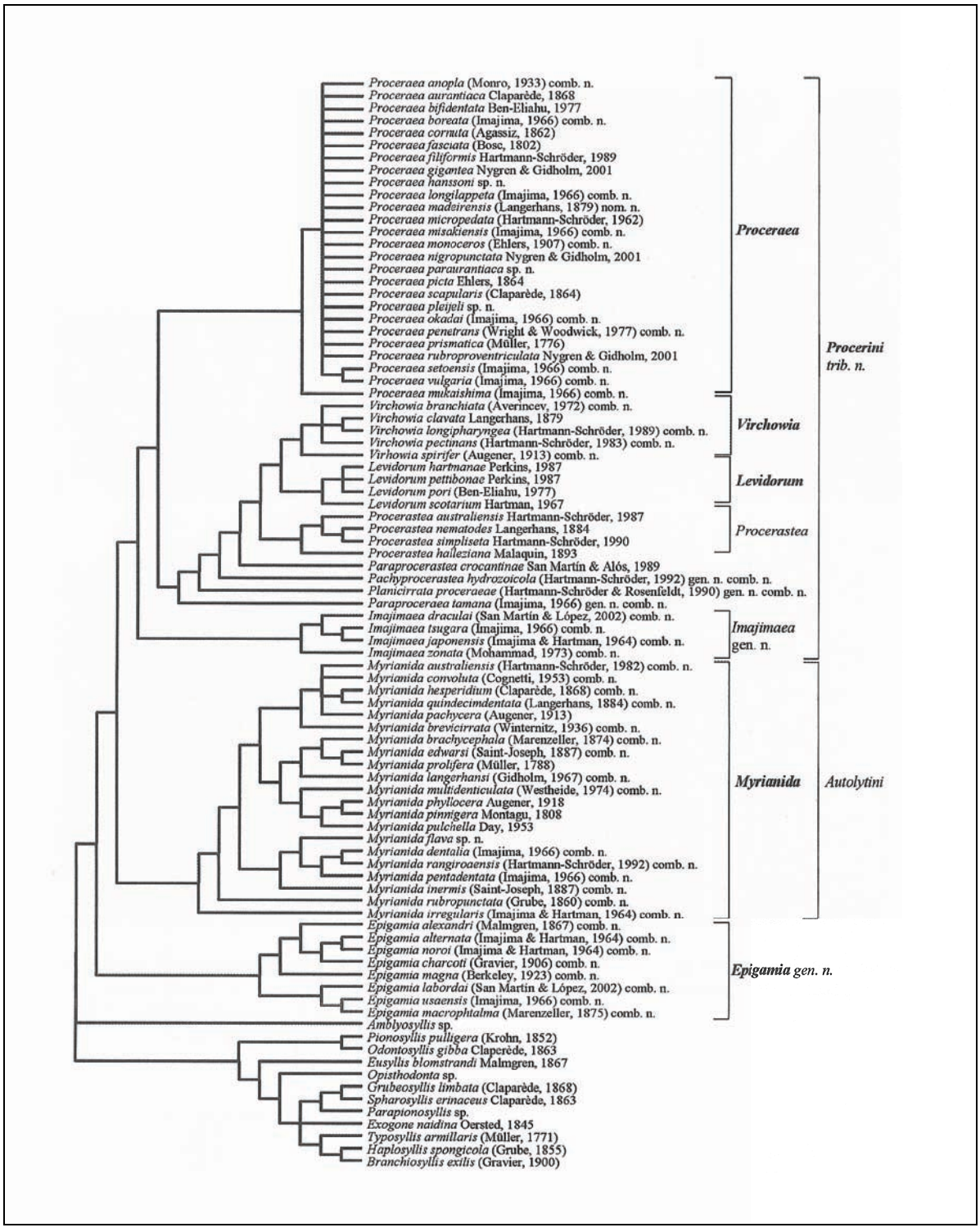


Figura 7. Consenso estricto del análisis combinado de datos moleculares y morfológicos llevado a cabo por Nygren (2004). (Tomado de Nygren, 2004).

II. La inferecia filogenética o Cladística

La reconstrucción o inferencia filogenética es el proceso por el cual mediante la aplicación de un conjunto determinado de técnicas y metodologías, obtenemos una hipótesis sobre las relaciones genealógicas o evolutivas entre los organismos objeto de estudio (Arnedo, 1999). El cladismo es la metodología de la sistemática filogenética formulada por Hennig (1966) y reformulada por Eldredge y Cracraft (1980) y Wiley (1981) que pretende dotar a las clasificaciones de los organismos de sentido evolutivo. La clasificación, según la cladística, debe reflejar el proceso evolutivo seguido por los organismos, más concretamente el orden de ramificación observado en sus filogenias. La incorporación de la filogenia en la clasificación permite que las categorías clasificatorias dejen de ser abstracciones ideales para convertirse en entidades reales que expresan la historia evolutiva de los organismos. Los grupos formados son predecibles y, pueden ser refutados con la aportación de nuevas evidencias filogenéticas.

Dado que una parte de esta tesis consiste en un estudio filogenético de la familia Syllidae, hemos considerado conveniente incluir algunos conceptos básicos de la terminología cladística para así facilitar su lectura.

1. Conceptos básicos

Un **carácter** es una característica, una parte observable o un atributo de un organismo (morfológico, molecular, etológico, ecológico, biogeográfico) que puede ser adecuadamente descrito o definido, cuyas diferentes manifestaciones se denominan **estados**. Existen dos tipos de caracteres: los homólogos y los homoplásicos. Dos caracteres son **homólogos** si están relacionados evolutivamente, de tal forma que derivan filogenéticamente del mismo estado en el ancestro común más cercano. Por otro lado, dos caracteres son **homoplásicos** si no están relacionados evolutivamente, es decir, si provienen de transformaciones independientes de un carácter anterior. Pueden distinguirse tres tipos de homoplasias: **convergencia**, si el estado homoplásico proviene de distintos estados ancestrales; **paralelismo**, si el estado homoplásico proviene del mismo estado ancestral; o **reversiones** cuando un estado se transforma en otro evolutivamente anterior. Los caracteres basados en secuencias nucleotídicas presentan una forma adicional de homoplasia. Dado que tan sólo existen cuatro caracteres o estados posibles

(A; T; G; C), la probabilidad de compartir un mismo carácter por cambios independientes es extremadamente alta.

En cladismo se distinguen dos tipos de caracteres homólogos (Fig. 8): las **plesiomorfías** o caracteres plesiomórficos, que son los caracteres primitivos; y las **apomorfías** o caracteres apomórficos, que son los caracteres derivados. Si el carácter es compartido por más de un taxón, entonces se denominan **simplesiomorfía** o **sinapomorfía**, respectivamente. Una **autapomorfía** es un estado apomórfico presente en un único taxón.

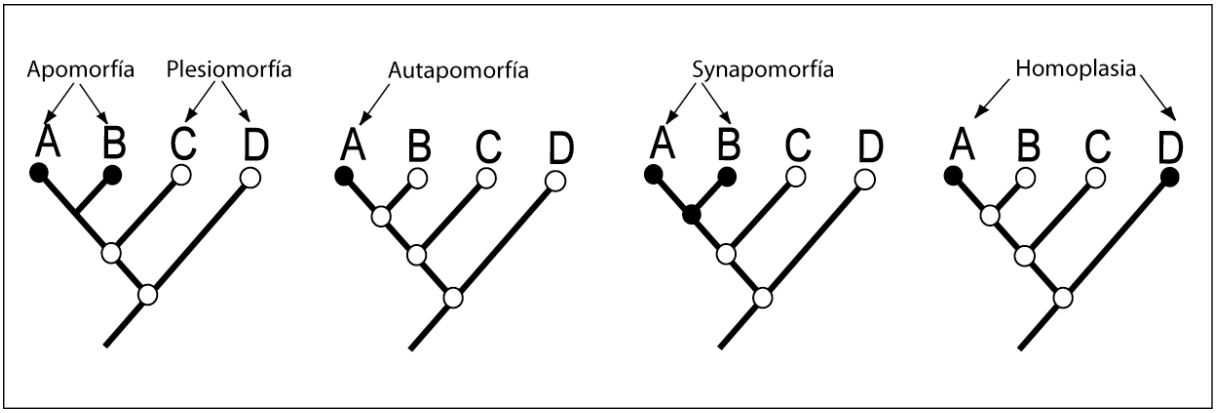


Figura 8. Terminología usada para describir las diferentes reconstrucciones de los estados ancestrales (○) y derivados (●). (Modificado de Page y Holmes, 1998).

Un **grupo monofilético** es un conjunto de taxones que comparten una apomorfía, es decir una sinapomorfía, por lo tanto contiene a todos los descendientes de un mismo antecesor. Un **grupo parafilético** es un conjunto de taxones con un plesiomorfía en común, es decir una simplesiomorfía. Incluye a un ancestro común y algunos de sus descendientes, pero no todos. Por último, un **grupo polifilético** es un grupo de taxones agrupados por la presencia de un carácter homoplásico. Es un grupo en el que el ancestro más reciente no es miembro de este grupo. Los tres tipos de grupos pueden verse sobre un cladograma hipotético en la figura 9. Sólo los grupos monofiléticos o clados constituyen grupos naturales y, por tanto, son los únicos que tienen importancia filogenética. Los grupos parafiléticos y polifiléticos existen exclusivamente a nivel metodológico. Una información más detallada sobre conceptos básicos de cladística puede consultarse en Arnedo (1999), Kitching *et al.* (1998) y Morrone (2000).

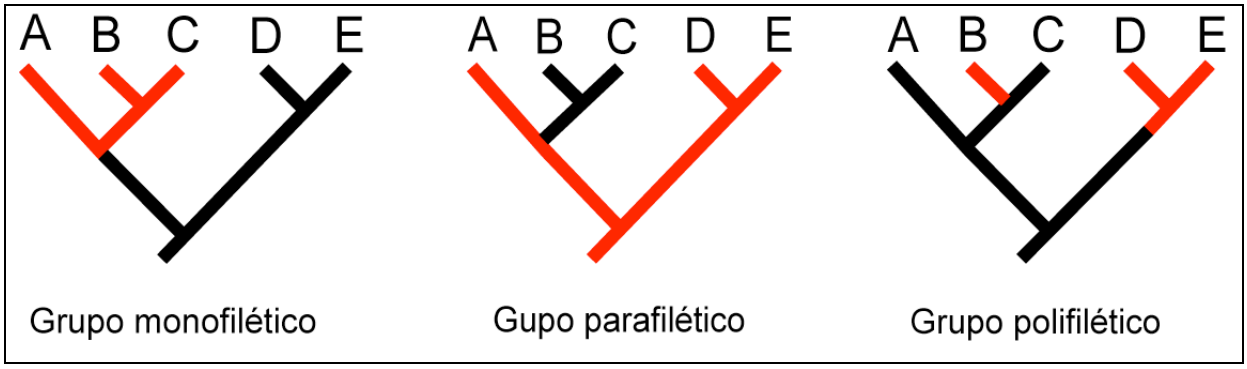


Figura 9. Representación de grupos monofilético, parafilético y polifilético en un cladograma hipotético.

Para poder determinar qué estados son plesiomórficos y cuáles son apomórficos, se pueden utilizar varios criterios, de entre ellos **la comparación con el grupo externo** es el más utilizado. De todos los caracteres (o estados) establecidos en un grupo monofilético, aquel que pueda encontrarse en su grupo hermano, corresponderá al estado plesiomórfico, mientras que el que se encuentre exclusivamente en el grupo interno será el apomórfico (Arnedo, 1999). Otro criterio usado tradicionalmente es el **criterio ontogenético**. El orden de aparición de los caracteres (=estados) durante la ontogenia del organismo, corresponde con la polaridad y, por tanto permite distinguir las sinapomorfías ("la ontogenia recapitula la filogenia"). Un criterio adicional es la **secuencia estratigráfica** en el cual la polaridad se obtiene a partir de la observación de la secuencia de aparición de los caracteres en el registro fósil.

La recuperación de las relaciones filogenéticas de un grupo consiste en evaluar el conjunto de los caracteres definidos para dicho grupo y distinguir cuáles representan sinapomorfías. Al proceso de selección y evaluación de los caracteres de los taxones estudiados se le denomina **análisis cladístico**. El resultado de este análisis es la elaboración de un cladograma, que consiste en un diagrama en forma de árbol donde se representan la distribución de los distintos caracteres y los grupos que definen. La interpretación de las ramificaciones como fenómenos de especiación y de los nodos internos como antepasados convierte al cladograma en una **filogenia**.

Todo análisis filogenético debe estar sometido a la construcción de un esquema racional, y por tanto, no arbitrario. Tal esquema debe estar en todo momento disponible a su refutación o a su confirmación, al introducir nuevos caracteres o taxones.

2. Las metodologías filogenéticas.

Los principios básicos de la cladística hennigiana se han ido desarrollando al mismo tiempo que las innovaciones tecnológicas han permitido la incorporación de los ordenadores y la adquisición de nuevos datos como los moleculares. Actualmente existen distintas metodologías filogenéticas. Todas ellas comparten la asunción de los grupos monofiléticos como los indicadores de las relaciones evolutivas; sin embargo, difieren profundamente en la manera en la que manejan los datos y se construyen los árboles.

Los principales métodos de análisis son: 1) Los métodos de distancias; y 2) Los métodos discretos, que a su vez se dividen en a) el análisis de parsimonia; b) el análisis de máxima verosimilitud ("maximum likelihood"); y c) el análisis bayesiano o "bayesian".

2.1. Los métodos de distancias

Estos métodos consisten en relacionar la distancia entre taxones, entendida como una medida de su disimilaridad, con su relación filogenética. Estas metodologías son los últimos remanentes de la escuela fenética, que no distingue entre homología y homoplasia, por lo que no son aptas para la reconstrucción filogenética basada en datos morfológicos. Sin embargo, se han puesto en práctica ampliamente con datos moleculares, ya que es posible utilizar modelos evolutivos que corrigen la estimación de las distancias en función de la homoplasia existente. Estos métodos transforman la matriz de caracteres en una matriz de distancias a partir de la cual construyen árboles. Algunos de los métodos de distancias más usados son el "UPGMA" o el "Neighbor-Joining".

2.2. Los métodos discretos

Estos métodos trabajan directamente con los caracteres, a diferencia de los métodos de distancias que trabajaban con la distancia entre taxones. Existen varias metodologías, de entre las cuales **el análisis de parsimonia** es, probablemente, la más utilizada.

Otras metodologías discretas que se han desarrollado fundamentalmente a raíz de la utilización de los datos moleculares son: El análisis de máxima verosimilitud ("Maximum likelihood") y la inferencia bayesiana o "bayesian". En ambos casos, la reconstrucción filogenética se considera un problema de probabilidades estadísticas.

El análisis de maxima verosimilitud: ML (Felsenstein, 1981) calcula la probabilidad de obtener los datos observados dado un árbol filogenético dado un modelo evolutivo. De entre todas las explicaciones posibles para los datos, se escogerá como la mejor aquella que hace a los datos observados los más probables. Se han ido elaborando multitud de modelos evolutivos de complejidad creciente, de entre los que el modelo más sencillo (JC; Jukes y Cantor, 1969) considera que todos los cambios entre nucleótidos (o aminoácidos) son igualmente probables. Se suman las probabilidades de todas las posibles reconstrucciones dando la verosimilitud o "likelihood" de cada sitio particular. El árbol final es el producto de las verosimilitudes de cada posición. Modelos evolutivos más complejos suponen que la frecuencia de las transiciones y las transversiones no es siempre igual y que las frecuencias nucleotídicas en diferentes taxones tampoco son uniformes.

La inferencia bayesiana (Rannala y Yang, 1996) está basada en el cálculo de la probabilidad posterior, es decir, en probabilidades que son estimadas después de adquirir conocimiento previo de los datos. La mejor estima filogenética es aquella que maximiza la probabilidad posterior de que un árbol sea el correcto. Para calcular la probabilidad posterior de un árbol se utiliza el Teorema de Bayes, que combina la probabilidad previa de una filogenia con su verosimilitud. El cálculo de la probabilidad posterior implica evaluar todos los posibles árboles y, para cada árbol, investigar todas las posibles combinaciones de longitud de rama y parámetros de modelo. El uso de este método está incrementándose recientemente, principalmente porque presenta las mismas ventajas que el ML, pero es mucho más rápido y permite, además de los moleculares, incorporar datos morfológicos.

Se explica a continuación, de una manera más detallada el método del análisis de parsimonia ya que es esta metodología la que se ha puesto en práctica en la tesis doctoral.

3. El análisis de Parsimonia

El principio de parsimonia es el criterio metodológico adoptado por el cladismo para decidir, en un análisis filogenético que presenta incongruencias entre los caracteres, cuál de los cladogramas posibles, el llamado árbol más corto, constituye la reconstrucción más probable que es representativa de la filogenia del grupo. El principio básico de la parsimonia es el denominado "navaja de Ockham", el cual establece que: "… dadas distintas soluciones posibles a un problema, la solución más económica es la preferible" (Scotland, 1992). La

hipótesis más parsimoniosa es, por tanto, la que explica la totalidad de los datos con el menor número posible de cambios (Wiley, 1981). El método busca un árbol (o conjunto de árboles) que minimizan la cantidad de cambio evolutivo, aquél o aquellos que requieren un menor número de cambios para explicar las diferencias entre los taxa. El principio de parsimonia puede ser calificado como un método hipotético deductivo.

La aplicación del criterio de parsimonia requiere contabilizar el número de transformaciones entre caracteres (o estados) en el árbol a evaluar, lo cual a su vez requiere asignar un determinado carácter (o estado) a los nodos internos correspondientes, es decir a los antepasados hipotéticos. Esto se lleva a cabo de manera que el carácter (o estado) asignado minimice el número de transformaciones (Arnedo, 1999).

3.1. Construcción de Cladogramas

Para poder hacer uso de algoritmos computacionales, los datos se presentan en forma de una matriz. Por convención, los nombres de los taxones se colocan como filas, mientras que los caracteres, como columnas.

3.1.1. La elección de los taxones

La selección de los taxones para un análisis filogenético suele depender del nivel taxonómico al que se quiere realizar el estudio. Si se pretende elaborar un análisis que compruebe la monofilia de una familia, cuanto mejor esté representada dicha familia, incluyendo representantes de todos los grupos internos, el análisis será más resolutivo. Si se pretenden estudiar las relaciones filogenéticas y la monofilia de las subfamilias, todas ellas deberán estar bien representadas en el análisis. Los análisis a un nivel genérico suelen incluir un representante de cada género, por lo general el género tipo. Sin embargo, muchas veces el genotipo no es la especie más representativa del género o no es la especie para la que se tiene más información, en tales situaciones, otra especie puede ser seleccionada para representar el género. Por otro lado, si el objetivo del análisis es conocer las relaciones filogenéticas de una nueva especie con las especies afines, entonces todas las especies del género (si éste se ha demostrado previamente que es monofilético) deberían ser incluidas.

La elección del grupo externo o “outgroup” suele plantear más problemas. Por lo general se elige como grupo externo al grupo hermano del grupo de estudio o “ingroup”, pero a

menudo es difícil conocer con certeza este grupo. El grupo hermano presentará una o más sinapomorfías compartidas con el grupo de estudio (Nixon y Carpenter, 1993). Hay pocos estudios que soporten claramente las relaciones filogenéticas entre grandes grupos por lo que la elección del grupo externo se complica dependiendo de los análisis previos que consideremos. La elección del grupo externo puede modificar la relación con el grupo interno por lo que generalmente, se incluyen varios grupos externos. En este caso, es aconsejable incluir algunos caracteres que resuelvan las relaciones entre los grupos externos.

3.1.2. Codificación de caracteres

La elección y la codificación de los caracteres es probablemente la fase más importante de todo el análisis cladístico. Si los caracteres han sido erróneamente seleccionados o codificados, todo lo que se desprenda de ellos, aunque el análisis cladístico esté bien elaborado, será falso.

Los caracteres pueden ser de dos tipos: **Caracteres binarios**. Aquellos que están constituidos por dos estados (generalmente representados por 0-1). Uno de ellos representa el estado plesiomorfo y el otro el apomorfo. La transformación entre un estado y el otro puede estar fijada a priori, entonces se conoce como par ordenado. **Caracteres multiestado.** Aquellos que presentan más de dos estados en su serie de transformación, y cuyas relaciones o conexiones de transformación de un estado a otro pueden ser desordenadas u ordenadas. Las transformaciones serán desordenadas cuando cada estado pueda transformarse directamente en otro estado, contándose como un paso en cualquiera de las transformaciones: 0-1, 1-2, 2-3, 2-1, 3-1, 3-0, etc. Sin embargo, serán ordenadas o aditivas cuando al pasarse sucesivamente de un estado a otro (0-1-2), cada transformación se contabilice como un paso.

La utilización de estados binarios y/o multiestados y/o la combinación de ambos tipos genera numerosas posibilidades de codificación. Pleijel (1995) resumió estas posibilidades en cuatro métodos diferentes de codificación (métodos A-D) (ver a continuación) para las diferentes expresiones morfológicas en las que puede aparecer una estructura (Fig. 10).

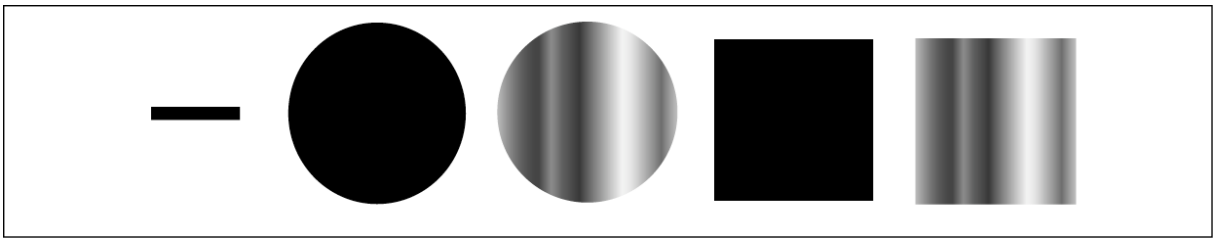


Figura 10. Posibles diferentes expresiones de una estructura. De izquierda a derecha: ausente, redondo y negro, redondo y rayado, cuadrado y negro, cuadrado y rayado. (Modificado de Pleijel, 1995)

Métodos de codificación:

A. 1. Carácter X: ausente (0)/ redondo y negro (1)/ redondo y rayado (2)/ cuadrado y negro (3)/ cuadrado y rayado (4)

B. 1. Carácter X: ausente (0)/ redondo (1)/ cuadrado (2)
2. Carácter X: ausente (0)/ negro (1)/ rayado (2)

C. 1. Carácter X: ausente (0)/ presente (1)
2. Carácter X: redondo (0)/ cuadrado (1)
3. Carácter X: negro (0)/ rayado (1)

D. 1. Carácter X: ausente (0)/ presente (1)
2. Forma redonda: ausente (0)/ presente (1)
3. Forma cuadrada: ausente (0)/ presente (1)
4. Coloración negra: ausente (0)/ presente (1)
5. Coloración distribuida en rayas: ausente (0)/ presente (1)

Cada uno de estos métodos presenta ventajas y desventajas, la elección de un método de codificación frente al resto puede atender a distintos criterios (Pleijel, 1995; Wilkinson, 1995; Kitching *et al.*, 1998; Strong & Lipscomb, 1999):

El método D es el único que evita tener que redefinir los caracteres cada vez que se añaden a la matriz diferentes combinaciones de los mismos. Sin embargo, en este método, al igual que en el método B, el estado "ausencia" recibe un mayor peso porque se repite cuando se trata de la misma característica, por lo que los grupos apoyados por este estado, serán

artificialmente favorecidos frente al resto. Además, en el método D, el número de caracteres necesarios para describir una estructura compleja puede ser muy elevado, pudiendo resultar en un sobrepeso que será mayor cuantos más caracteres usemos para definirla. El método C soluciona estas dificultades, sin embargo adolece del problema de los "inaplicables". Los "inaplicables" surgen cuando una estructura compleja está ausente en un taxón. Del conjunto de caracteres que hacen referencia a una misma estructura, sólo el primero podrá ser codificado como "ausente", en los demás normalmente se añade "-" para indicar que no es posible su codificación. Sin embargo, hasta el momento, no existen programas informáticos que distingan los "inaplicables" (-) de los datos desconocidos (?), por lo que la posición de los taxones con "inaplicables" en la filogenia puede verse afectada (Strong & Lipscomb, 1999). Por último, en los métodos A y B, sólo uno de los estados definidos puede ser asignado a un nodo interno o ancestro. Sin embargo, en los métodos C y D, cada carácter se separa en varios, por lo que el antepasado puede presentar una combinación no observada en ninguno de los taxones terminales (Arnedo, 1999).

Existen, por tanto, criterios a favor y en contra de cada uno de los distintos métodos de codificación. La elección del tipo de codificación es muy importante y, a menudo, no se ha llevado a cabo de manera consistente. Es frecuente observar una mezcla de todos estos métodos en el mismo análisis cladístico sin justificación previa. A menudo el problema radica en nuestro desconocimiento acerca de muchas estructuras y de sus relaciones de dependencia biológica (Wilkinson, 1995). El método C parece ser uno de los más utilizados en estudios filogenéticos de poliquetos (Nygren, 1999; 2004; Santos *et al.*, 2005; Zanol *et al.*, 2007; Nygren & Pleijel, 2007) porque permite contrastar la información de cada taxón y reconstruir la evolución de los caracteres, sin embargo presenta el problema de los "inaplicables" que es, por el momento, de difícil solución.

3.1.3. Datos moleculares y alineamiento de las secuencias

Los datos moleculares están resultando ser una herramienta muy útil para la elaboración de hipótesis evolutivas en muchos grupos de organismos (Bleidorn *et al.*, 2003a, b) y su utilización también se ha extendido recientemente al campo de los anélidos poliquetos. Entre los genes que se usan para elaborar análisis filogenéticos en anélidos, el gen nuclear 18S rDNA ha sido ampliamente utilizado para estimar las relaciones entre los grandes grupos, tales como las familias en poliquetos o incluso relaciones con oligoquetos e hirudíneos (e. g. Apakupakul *et al.*, 1999; Martin *et al.*, 2000; McHugh, 2000), pero también se ha utilizado

para estimar las posibles relaciones entre taxones más cercanos como especies o géneros (Nygren and Sundberg, 2003; Siddall *et al.*, 2005). Por otro lado, los genes mitocondriales como el gen de la citocromo oxidasa (COI) o el 16S, tienden a acumular mutaciones más rápido que los nucleares, por lo que se utilizan generalmente para inferir relaciones cercanas dentro del grupo interno (Folmer *et al.*, 1994; Wiklund *et al.*, 2005). Otros genes nucleares (28S, H3) y mitocondriales (EF-1α, 12S, citocromo B) han sido también utilizados en filogenias de anélidos, aunque en menor medida (McHugh, 1997; Brown *et al.*, 1999; Colgan *et al.*, 2001; Rousset *et al.*, 2003, 2004). Halanych y Janosik (2006) hacen una exhaustiva recopilación de los distintos genes que se han utilizado para inferir relaciones filogenéticas en anélidos.

Cuando se utilizan datos moleculares, cada una de las posiciones (nucleótidos), una vez alineadas las secuencias, va a representar un carácter. El alineamiento de las secuencias es, por tanto, fundamental a la hora de establecer correctamente las regiones homólogas de las secuencias para su comparación (homología de posición). Sin embargo, la definición del alineamiento que mejor se ajuste a los datos puede ser problemática, debido a que las secuencias pueden acumular multitud de sustituciones, inserciones, delecciones y zonas de repetición a lo largo del tiempo (Higgins, 2003).

Se han desarrollado numerosos programas informáticos que realizan los alineamientos dados unos valores de penalización para la inserción y longitud de espacios en las secuencias ("gaps"). La metodología mayoritariamente empleada para realizar alineamientos múltiples consiste en elaborar una matriz de distancias de las secuencias y a continuación, obtener un árbol guía. El alineamiento múltiple se construye siguiendo el orden de ramificación del árbol. El problema fundamental que presenta esta metodología consiste en que el alineamiento final puede variar dependiendo del árbol que se usa de partida para construirlo. Los alineamientos finales deben además ser supervisados a mano (Grande, 2004).

Una forma de mejorar la calidad de los alineamientos es la incorporación, en caso de que exista, de información estructural. Así, por ejemplo, los genes ribosómicos tienen estructura secundaria en la molécula transcrita, con zonas complementarias (stems) y zonas de cadena sencilla (loops). El reconocimiento de las zonas complementarias en la secuencia puede resultar de gran ayuda en la determinación de posiciones homólogas. Sin embargo, hay ocasiones en que la divergencia entre las secuencias es tan grande que la asignación de homología se ve seriamente comprometida. Llegados a este punto, la mejor opción es simplemente eliminar estas zonas del análisis posterior (Arnedo, 1999).

En las matrices de datos moleculares, los “gaps” introducidos para generar el alineamiento plantean un problema similar al de los “inaplicables” en los caracteres morfológicos. Por lo general los “gaps” se tratan de la misma manera que la información desconocida “missing data” (?) pero hay autores que sugieren que pueden ser considerados como un quinto estado (A, T, C, G, -). Sin embargo, este criterio tiene el inconveniente de que cada “gap” es considerado como un carácter independiente (cuando puede no serlo, p. ej. en una inserción/delección múltiple) resultando en una sobrevaloración de los grupos apoyados por los mismos (Arnedo, 1999).

3.1.4. Criterios de optimización.

El criterio que se usa para determinar a priori el número de pasos entre cada uno de los estados de un carácter se denomina optimización. La elección de uno u otro método afecta a la topología final del árbol así como a su longitud total.

Optimización de Farris (Kluge y Farris, 1969; Farris, 1970). Los estados pueden revertir a su condición plesiomórfica, por lo que el cambio de 0-1 vale el mismo número de pasos que de 1-0. Los caracteres multiestado son aditivos, por lo que si 0-1 vale un paso y 1-2 vale un paso, 0-2, valdrá dos pasos.

Optimización de Fitch (Fitch, 1971). Trata a los caracteres multiestado como no aditivos o desordenados, es decir que si 0-1 vale un paso y 1-2 vale un paso, 0-2 también valdrá un paso.

Optimización de Camin-Sokal (Camin y Sokal, 1965). Este modelo asume la irreversibilidad, es decir, una vez que se adquiere una estructura, ésta no puede ser perdida, por lo que el cambio1-0 no es posible.

Optimización de Dollo (Farris, 1977). Este modelo sólo acepta las reversiones y excluye las convergencias. Asume que ciertas estructuras complejas (como el ojo de los vertebrados) no pueden evolucionar más de una vez, por lo que la homoplasia sólo puede tratarse como reversión. Prohíbe, por tanto, los paralelismos, por lo que los cambios 0-1 se producirá una sola vez.

3.2. Búsqueda del árbol más parsimonioso

Una vez que se ha construido la matriz de datos, se han codificado los caracteres, y se ha establecido el tipo de optimización a seguir, el siguiente paso es la búsqueda del árbol más parsimonioso o "most parsimoniosus tree", es decir, aquel o aquellos árboles que minimizan el número de pasos requeridos para explicar una matriz o conjunto de datos.

Los criterios de resolución para establecer el árbol más parsimonioso a partir de un conjunto de datos han ido modificándose a lo largo del tiempo. Inicialmente, el procedimiento fue propuesto por Hennig, y su aplicación resultaba relativamente simple para un reducido número de taxones. El procedimiento consistía en la adición secuencial de cada carácter a una topología inicial sin resolver para el conjunto total de los taxones a analizar; la topología del árbol iba progresivamente resolviéndose a medida que avanzaba dicha adición secuencial. Con la aparición de los algoritmos numéricos, los análisis se llevan a cabo de forma inversa. En este caso, son los taxones los que se adicionan secuencialmente teniendo en cuenta todos los caracteres. Estos procedimientos se realizan en árboles sin raíz, pues el número de sus topologías es menor que el de sus correspondientes árboles enraizados. El enraizamiento se realiza una vez finalizado este análisis según distintos criterios, p.e. la comparación con un grupo externo.

El problema es que con *n* taxones terminales se pueden construir (2n-3)! /[2n-2 (n-2)!] árboles dicotómicos (para n=10 existen aproximadamente 3,5 x 107 árboles). Por lo que la búsqueda de todos los árboles posibles (algoritmos exactos), para después elegir el más corto, es sólo posible con un número reducido de taxones. Para trabajar con un número elevado de taxones hay que trabajar con algoritmos heurísticos.

3.2.1. Algoritmos exactos

Los algoritmos exactos son aquellos por los que se garantiza la obtención de todos los árboles más parsimoniosos correspondientes a una matriz dada. Su aplicabilidad está limitada a unos 20 taxones terminales.

Los algoritmos exactos pueden ejecutarse por medio de un análisis exhaustivo o por la técnica de “Branch and bound”. Los **métodos exhaustivos** evalúan todos los árboles posibles, siempre que el conjunto de especies no sea superior a 10. El método “**Branch and bound**” (Hendy y Penny, 1982; Swofford y Olsen, 1990) consiste en un algoritmo exacto que se

utiliza cuando el número de taxones esta comprendido entre 20 y 30. Esta técnica permite una búsqueda exhaustiva, pero referida a un árbol determinado, el cual puede ser elegido al azar, o calculado a partir de un algoritmo heurístico (ej. el algoritmo de Wagner). A partir de la selección de este árbol se determina el número de pasos, de forma que el árbol "mínimo" no pueda exceder la longitud de este árbol de referencia.

3.2.2. Algoritmos heurísticos.

Estos algoritmos heurísticos se utilizan cuando resulta imposible aplicar los algoritmos exactos, y por tanto, sólo queda la posibilidad de una aproximación al mejor resultado posible. Poseen la ventaja de obtener un resultado en un tiempo de cálculo razonable, sin embargo, no se tiene la certeza de que sean los más parsimoniosos, ni que todos los árboles más parsimoniosos hayan sido localizados.

Entre los métodos heurísticos más utilizados está la "**adición paso a paso**" (**stepwise addition**), que consiste en la incorporación secuencial de los taxones. Este método construye un árbol preliminar seleccionando tres taxones al que va añadiendo de manera paulatina los restantes. Existen distintos criterios para elegir los taxones iniciales (los tres primeros de la matriz, o por azar, o se elige uno por azar y se calculan los dos de menos distancia, o se calculan todos los árboles posibles de tres taxones y se selecciona el más corto). Una vez conseguido el árbol o árboles iniciales, se intenta conseguir un árbol mejor (con menor número de pasos) mediante el desplazamiento de sus ramas, es decir mediante el denominado "**reordenamiento de ramas**" (**branch swapping**). Si una reordenación genera un árbol más corto, éste es el utilizado para una nueva reordenación, de esta forma se puede llegar a alcanzar el árbol más corto. Las reordenaciones más utilizadas (Swofford *et al.*, 1996) por los programas de ordenador son: "**Nearest neighbour interchange" (NNI)**, que consiste en seleccionar una rama interna e intercambiar los dos grupos que quedan a sus extremos. Esto se realiza en todas las ramas internas del árbol. "**Subtree pruning and regrafting" (SPR)**, que consiste en romper una rama interna del árbol original y posteriormente reubicarla en distintas posiciones. Se evalúan todas las posibles combinaciones de romper ramas y reubicarlas en nuevas posiciones. "**Tree bisection and reconnection" (TBR)**, que es similar al anterior en que también se separa una rama interna del árbol, pero, antes de reubicarla se enraíza. Se evalúan todas las posibles combinaciones posibles de romper ramas internas, todos los re-enraizamientos y reconexiones posibles hasta encontrar el árbol o árboles más cortos. Este último método es el más utilizado.

Como se ha señalado previamente, los métodos heurísticos no garantizan la obtención del árbol más corto. Obtienen los árboles más cortos derivados de unos árboles iniciales que se conocen con el nombre de "mínimo local". Si alguno de los mínimos locales coincide con un "mínimo global" (los más cortos de todos), entonces se habrá encontrado al menos uno de los árboles más parsimoniosos posibles (Arnedo, 1999). Sin embargo es imposible tener la certeza de que esto haya ocurrido. El árbol o conjunto de árboles más cortos encontrados se conocen como "máximo" o "máximos locales", que no tiene por qué coincidir con el máximo global.

Otro problema es el de las islas de árboles. "Una isla es un conjunto de topologías de árboles de la misma longitud en el cual cada miembro está conectado con los otros por una serie de árboles y difiere de otro miembro del conjunto en tan solo una simple combinación" (Maddison, 1991; Page & Holmes, 1998). Es decir, las islas de árboles están separadas unas de otras por una sola reordenación de ramas. El problema surge cuando los árboles más parsimoniosos pertenecen a islas diferentes. Cada isla vendrá determinada por el tipo de reordenación (NNI, SPR o TBR) y, como cada búsqueda utiliza un sólo árbol preliminar y un tipo de reordenación, no será posible encontrarlos todos.

Existen metodologías que intentan eliminar el problema de las islas de árboles. Una de ellas es conocida como "**The parsimony ratchet**" (Nixon, 1999). El "**ratchet**" es un método que combina el TBR con una técnica específica que permite encontrar más de un óptimo local. Cuando el TBR encuentra un óptimo local, el ratchet modifica los datos iniciales (duplicando un subconjunto de datos elegido al azar, dándole peso a los caracteres, etc.) y vuelve a aplicar el protocolo del TBR. Cuando la nueva búsqueda encuentra otro máximo local, el conjunto de datos vuelve a sus valores originales y se repite de nuevo el proceso tantas veces como se le indique al programa. El ratchet es muy eficiente para matrices muy grandes, en estos casos consigue además reducir considerablemente el tiempo de búsqueda (Nixon, 1999).

3.3. Árbol de consenso

En ocasiones, un mismo conjunto de datos puede resultar en más de un árbol igualmente parsimonioso. En estos casos se busca un árbol de consenso que represente las partes concordantes entre los distintos árboles.

Existen varios métodos de consenso. **El consenso estricto** (Nelson, 1979; Sokal y Rohlf, 1981) combina únicamente aquellos componentes que aparecen repetidamente en todos los cladogramas originales. **El consenso semiestricto** (Bremer, 1990) incluye aquellos componentes que no están en contradicción con ningún otro componente de los cladogramas originales; es decir, incluye los componentes del consenso estricto junto con aquellos que resulten compatibles entre todos los cladogramas. **El consenso de Nelson** (Nelson, 1979; Page, 1989) incluye los conjuntos de componentes compatibles que aparecen con más frecuencia. **El consenso de Adams** (Adams, 1972) coloca a los taxones que producen conflicto en el nodo donde todas sus posiciones coinciden. **El consenso de mayoría** (Margush y McMorris, 1981) resulta de combinar aquellos componentes que aparezcan en la mayoría (>50%) de los cladogramas originales.

En general, el árbol de consenso es menos resolutivo, de mayor longitud y menos informativo que los árboles iniciales. Esto es debido a que los caracteres del árbol de consenso tienden a cambiar más veces que en un árbol cualquiera. Debe destacarse que ningún árbol de consenso es la hipótesis más idónea para el conjunto de los datos, sino que debe interpretarse como el grado de acuerdo o desacuerdo entre varios árboles obtenidos después de una búsqueda y no como un árbol filogenético.

3.4. Estadísticos descriptivos

Existen varios estadísticos que permiten cuantificar la cantidad de información filogenética y el grado de homoplasia en un cladograma (Kitching *et al.*, 1998; Morrone, 2000). Estos estadísticos nos permiten comparar distintos árboles, aunque éstos difieran en su topología.

- Longitud. La longitud de un cladograma es el número de pasos necesarios para mantener las relaciones genealógicas entre los taxones del mismo (Camin y Sokal, 1965). Los cladogramas más simples o más parsimoniosos serán los de menor número de pasos o los más cortos.

- Índice de consistencia: CI (Kluge y Farris, 1969). Este índice es una estimación de la cantidad de sinapomorfías y del grado de homoplasia. El índice de consistencia de un árbol es igual a la relación entre el número mínimo (R) de transformaciones necesarias para los estados de todos los caracteres (número mínimo de pasos) y el número real de

transformaciones (L) en el árbol considerado. En el árbol más parsimonioso, L representa la longitud mínima del árbol.

$$CI = R / L$$

Valores iguales a 1 indican ausencia de homoplasia y la diferencia L-R representa el número de homoplasias. El valor de este índice puede verse aumentado de manera artificial por la inclusión de autapomorfías o caracteres invariables, ya que éstos no apoyan ninguna agrupación y, por tanto siempre encajan perfectamente. Por lo general dichos caracteres no deben introducirse en el análisis.

- Índice de retención: IR (Farris 1989). Este índice cuantifica la homoplasia observada en un carácter en función de la homoplasia posible. El índice de retención de un árbol es igual a la mayor cantidad de pasos que puede tener un cladograma (G) menos el número real de pasos (L), dividido por el mayor número de pasos (G) menos el menor número posible de pasos de un cladograma (R).

$$RI = (G-L) / (G-R)$$

Valores altos de IR indican que los cambios se acumulan preferentemente en las ramas internas, mientras que los valores bajos sugieren sugieren que los cambios se acumulan en ramas terminales.

- Índice de consistencia rescalado: RCI (Farris, 1989). Resulta de multiplicar el índice de consistencia por el índice de retención:

$$RCI = IC \times RI$$

3.5. Pesado de caracteres

Consiste en dar peso a los caracteres a priori o una vez que se haya realizado el análisis para dotar a los caracteres de distinta importancia como indicadores de las relaciones filogenéticas. Existen distintas técnicas de pasado de caracteres, entre ellas la más conocida es la del **pesado sucesivo** (Farris, 1969). En esta técnica, el peso de un determinado carácter estará en función de su ajuste sobre el árbol o árboles resultantes de un análisis previo. Es decir, se parte de una situación inicial en la que todos los caracteres tenían el mismo peso y se obtiene un conjunto de cladogramas a partir de ellos. Al cuantificar la homoplasia resultante, se reasignan pesos y se hace un nuevo análisis. El proceso se repite hasta que el resultado sea

estable. Un posible inconveniente del pesado sucesivo es que al cambiar los pesos iniciales se puede llegar a una solución diferente (Goloboff, 1998). Goloboff (1993) propuso un método alternativo para pesar los caracteres. Este método permite calcular el peso de los caracteres simultáneamente a la búsqueda de árboles.

3.6. Grado de soporte de los clados en los árboles obtenidos

Existen pruebas estadísticas que nos permiten determinar la confianza en los resultados de un análisis cladístico (Felsenstein, 1985; Bremer, 1994; Siddall, 1995). Algunas de estas pruebas son:

- *Bootstrap*. Consiste en eliminar al azar la mitad de los caracteres de una matriz de datos, a continuación duplicarlos para obtener una nueva matriz del mismo tamaño que la original y analizar esta matriz para obtener los árboles más parsimoniosos (Felsenstein, 1985). El proceso se repite al menos 100 veces y el porcentaje de aparición de cada clado en el cladograma de consenso de bootstrap representa su índice de soporte. Valores de soporte por debajo de un 70% no son fiables.

- *Jacknife*. Es una prueba similar a la anterior. Consiste en eliminar al azar caracteres o taxones pero sin reponerlos (Farris *et al.*, 1996; Lanyon, 1985; Siddall, 1995). En este caso, al igual que en el "Bootstrap", valores de soporte por debajo de un 70% no son totalmente fiables.

- Soporte de ramas o *Bremer support* (Bremer, 1988, 1994). Este método examina los pasos extra necesarios para que se pierda una rama en el cladograma de consenso. Las ramas mejor soportadas obtendrán valores más altos.

- ***Symmetric resampling*** (Goloboff *et al*., 2003). Es un tipo de prueba muy similar al Jacknife pero consigue evitar los problemas que genera la introducción de caracteres con distinto peso en las pruebas tradicionales de soporte.

3.7. Combinación de datos de distinta naturaleza

Cada vez es más frecuente encontrar análisis cladísticos que trabajan con distintos tipos de información. Los análisis basados en datos morfológicos siguen siendo frecuentes pero cada vez son más comunes los análisis que incorporan información molecular (ADN, ARN, proteínas, etc.). El problema surge a la hora de plantearnos cómo congeniar los resultados que

obtenemos procedentes de fuentes de información tan diferentes. Se han propuesto distintas aproximaciones:

- Análisis particional o congruencia taxonómica. Esta aproximación considera que es mejor tratar las diferentes clases de datos de manera independiente y utilizar un consenso para representar gráficamente la información común (Arnedo, 1999). Se considera una manera óptima de presentar y discutir los resultados ya que los caracteres provienen de fuentes diferentes y, por tanto, es menos probable que apoyen la misma filogenia si esta es errónea (Miyamoto y Fitch, 1995). Resulta útil cuando no se puede aplicar el mismo método de inferencia a todos los datos.

- Análisis conjunto o evidencia total. Consiste en combinar todos los datos en una sola matriz y analizarlos conjuntamente (Kluge, 1998). Las principales ventajas de esta aproximación son que las hipótesis obtenidas están basadas en la máxima evidencia disponible y que los distintos conjuntos de datos pueden ofrecer información a distintos niveles filogenéticos. Además, un conjunto de datos con señal filogenética débil (p. e. debido a la presencia de mucha homoplasia) puede ver incrementada su señal por congruencia con otros caracteres de conjuntos distintos. Finalmente, los caracteres combinados en una sola matriz pueden ser reestructurados durante el análisis y apoyar clados que no se encontrarían en el análisis por separado (Arnedo, 1999). Cuanto más diversa sea la procedencia de los caracteres (p. ej. morfológicos, diferentes genes moleculares, biogeográficos, comportamentales, etc.), mayor será el poder explicativo del árbol obtenido, ya que éste derivará de una mayor cantidad de evidencia evolutiva (Kluge y Wolf, 1993). A pesar de ser ésta una aproximación con numerosas ventajas, el problema surge cuando no tenemos información de las distintas fuentes para todos los taxones por lo que la matriz puede quedar con numerosos interrogantes.

3.8. Ventajas y desventajas del análisis de parsimonia

Una crítica frecuente a la parsimonia consiste en suponer que la evolución deba transcurrir a través de los caminos más cortos y que las homoplasias tengan que ser fenómenos poco corrientes. Sin embargo, estas críticas no están bien fundadas, en primer lugar porque el análisis de parsimonia no dice que la evolución tenga que haber seguido los caminos más simples, lo que hace es elegir, de entre varias opciones, aquella que representa un menor

número de cambios. En segundo lugar, la parsimonia minimiza la homoplasia pero eso no quiere decir que la considere como algo raro o poco frecuente (Farris, 1983; Arnedo, 1999).

Otra crítica que encuentra más apoyo se conoce como la inconsistencia de la parsimonia o "The Felsenstein Zone" (Felsenstein, 1978). Se entiende como consistencia a la propiedad de converger en el árbol correcto cuando se muestrea un gran número de caracteres. En el método de la parsimonia, las ramas más largas tienden a atraerse como producto de la similitud resultado de la convergencia aleatoria de cambios homoplásicos, con lo que el resultado final no tiene por qué ser el árbol correcto. Sin embargo, este tipo de inconsistencias han sido igualmente demostradas en prácticamente todos los métodos de reconstrucción filogenéticos (Siddall, 1998).

Se ha discutido que la parsimonia que existe en la naturaleza no es completamente equivalente con la parsimonia aplicada por el cladismo. La parsimonia utilizada por esta corriente metodológica consiste básicamente en buscar los árboles evolutivos más cortos posibles. El problema está en que, habitualmente, los métodos cladistas usan caracteres de tipo 0, 1 (primitivo, derivado) y el cambio de 0 a 1 se realiza en un paso. Esto puede ser una excesiva simplificación de la realidad en la que no existen caracteres discretos tan sencillos, sino que en cualquier carácter que evoluciona intervienen multitud de procesos que no son tenidos en cuenta. Sin embargo, este problema parece estar más relacionado con la codificación de caracteres y con nuestro desconocimiento acerca de la morfología, fisiología, etología, etc. de muchos de los grupos de estudio. La parsimonia como metodología científica no puede solucionar estas carencias, sin embargo cuenta con las herramientas para que dicha información pueda ser incorporada a medida que la vayamos descubriendo.

Uno de los problemas que pueden surgir en las clasificaciones basadas en resultados cladísticos reside en su posible inestabilidad. Cada cladograma representa una hipótesis evolutiva global; ello lo convierte en algo cambiante ya que nuevos estudios pueden llevar a una nueva clasificación taxonómica, con cambios jerárquicos, por ejemplo por algo tan común como la entrada de una nueva especie. Para solucionar el problema sólo podemos continuar buscando caracteres que permitan acceder a nuevas fuentes de información, y que paulatinamente contribuyan a la elaboración de hipótesis filogenéticas más robustas y, por tanto, más estables. Otra crítica realizada al cladismo es que se está convirtiendo en un método automático de obtención de resultados, evitándose cualquier discusión de tipo

evolutivo y dejando todo en manos de los ordenadores. Pero evidentemente, la metodología no es culpable del insuficiente o mal uso que se pueda hacer de ella.

A favor del cladismo se ha argumentado que es un método científico y objetivo, en el sentido de proponer hipótesis refutables, con una metodología clara, sencilla e intuitiva; que las búsquedas de árboles son muy eficientes; y que está bien fundamentado filosóficamente (Arnedo, 2007).

III. Organización de la tesis

El estudio de una familia tan extensa en cuanto a número de especies como la Familia Syllidae resulta complicado. Como es materialmente imposible estudiar toda la familia de una vez y en una única tesis doctoral, tuvimos que seleccionar algunas problemáticas que nos parecieron representativas del estado actual de conocimiento. Presentamos, a continuación, una explicación previa a la estructura de la tesis que nos permita entender por qué éstos y no otros aspectos fueron seleccionados fueron seleccionados para desarrollar este trabajo.

La tesis doctoral está dividida en cuatro bloques diferentes. El primer bloque reúne resultados eminentemente taxonómicos, de ahí que los hayamos nombrado "**Bloque I. Estudio taxonómico de la Familia Syllidae**". Esta parte de la investigación está especialmente centrada en la resolución de algunos problemas de índole taxonómica de los que adolece el grupo. En primer lugar, los sílidos son un grupo ampliamente conocido pero cuyos estudios en determinadas áreas geográficas del planeta siguen siendo escasos. Por esta razón, decidimos continuar con los estudios ya comenzados varios años atrás por el equipo de investigación de la Universidad Autónoma de Madrid sobre la poliquetofauna del Parque Nacional de Coiba (Panamá), cuyo medio marino había sido totalmente desconocido hasta hace poco tiempo. Durante las expediciones científicas regulares a la Estación Biológica hispano-panameña, se recogió un abundante colección de muestras de sílidos intersticiales. El estudio de esta colección está incluido en esta tesis doctoral y se presenta como parte de los resultados.

Por otro lado, el Océano Pacífico, en concreto la costa Este del continente asiático y gran parte del Océano Indico, son otras áreas geográficas que, en general, han sido poco prospectadas. Para intentar solventar dichas lagunas nos propusimos estudiar material de sílidos de esas áreas. Específicamente tuvimos la oportunidad de estudiar una extensa colección de sílidos de Japón, gracias a la colaboración de nuestro colega Dr. E. Nishi, y una colección de sílidos de Indonesia recolectada durante la "Siboga Expedition" (1899-1900) que fue proporcionada por el Dr. Harry A. Ten Hove. En ambos casos, los resultados fueron sorprendentes; por un lado por el desconocimiento previo sobre la fauna de sílidos de estas áreas y por otro, por su enorme diversidad.

Durante el transcurso del estudio taxonómico de estas colecciones tuvimos la oportunidad de acceder a material del estado de California (EEUU) gracias a la colaboración del Dr. Arne

Nygren. La costa Oeste de Estados Unidos cuenta con varios estudios sobre poliquetos de entre los que destaca el catálogo de especies elaborado por Blake y Hilbig (1995). Sin embargo, entre el material estudiado encontramos una nueva especie del género *Opisthosyllis* que describimos y nos sirvió para abordar la revisión de las especies pertenecientes a dicho género que hasta el momento estaba desorganizado.

Por último, nos planteamos abordar otro tipo de problemas más cercanos en distancia geográfica pero que representan igualmente interrogantes aún por resolver en el conocimiento del grupo. Ya que nuestro conocimiento sobre los sílidos del Mediterráneo occidental era bastante completo (ver trabajos de San Martín, 1984, 2003), nos propusimos estudiar una colección de sílidos del Mediterráneo oriental, en concreto del Líbano (proporcionada por el Dr. Dieter Fiege); y así poder tener más datos para comparar ambas faunas. Al mismo tiempo resultó ser una oportunidad excelente para trabajar sobre hipótesis acerca de la migración de especies, en concreto migraciones Lessepsianas (entre el Mar Mediterráneo y el Mar Rojo).

Con el estudio en concreto de estas colecciones pretendimos abordar algunos de los múltiples problemas del grupo al mismo tiempo que adquiríamos un conocimiento práctico sobre la anatomía de los sílidos y una mayor destreza en los procesos de identificación.

El segundo bloque de esta tesis podría ser una continuación del primero en el sentido de que continúa siendo un estudio taxonómico de la familia Syllidae, pero, en este caso, los objetivos que nos marcamos fueron diferentes. En el **"Bloque II: Revisión de géneros de la Familia Syllidae**" reunimos los resultados de un proceso de exploración de los géneros de la familia Syllidae cuyas descripciones no eran completas o planteaban dudas taxonómicas. Muchos de estos géneros habían sido descritos hacía más de 50 años y no habían vuelto a encontrarse ejemplares similares desde entonces. Las técnicas, el equipo y el marco conceptual de la biología en su conjunto han experimentado una considerable mejora, gracias a ello, pudimos identificar estructuras y características que eran imposibles de discernir un siglo o medio siglo atrás.

Tanto para el desarrollo de los resultados incorporados en el Bloque I como para los del Bloque II fue preciso estudiar una enorme cantidad de material comparativo. Este material procedió en gran parte de las colecciones de sílidos de Australia que se encuentran actualmente en el Museo de Sydney. Este material ha sido estudiado por Guillermo San

Martín, Pat Hutchings y por la doctoranda, y ha sido de gran ayuda durante los procesos de identificación. De la misma manera, fue necesario y resultó enormemente útil como material comparativo el estudio de un gran número de series tipo depositadas en numerosos museos europeos. Las estancias de investigación en los museos de Historia Natural o de Zoología de París, Berlín, Ámsterdam, Hamburgo y Londres han jugado un papel muy importante en el desarrollo de esta investigación. Resultaron oportunidades excelentes para conocer una gran cantidad de series tipo de Syllidae, la mayoría de ellas descritas por notables autores en el estudio de poliquetos a lo largo de los últimos años del siglo XIX y las primeras décadas del XX (por ejemplo Grube, Augener, Ehlers, Gravier, Saint-Joseph, Quatrefages, Fauvel, Rullier, Amoreux, McIntosh, entre otros). En la mayoría de los estudios más actuales y de mayor contribución a la caracterización de las familias de poliquetos sigue siendo necesario recurrir a las series tipo, así como al conocimiento acumulado años atrás. En nuestro caso, la comparación con el material tipo formó parte fundamental del desarrollo de este trabajo.

El tercer bloque pudo elaborarse una vez que los bloques I y II estaban prácticamente terminados. Para el desarrollo de este tercer grupo de investigaciones precisábamos de la experiencia previa y del conocimiento adquirido durante las fases de identificación y revisión de especies y géneros. Necesitábamos partir de la taxonomía y de sus herramientas para poder componer un análisis filogenético basado en una metodología cladista. De esta manera se forjó el "**Bloque III: Revisión filogenética de la Familia Syllidae**". En este bloque nos marcamos objetivos relacionados con la historia evolutiva de la familia. Abordamos las preguntas desde dos fuentes de datos diferentes, por un lado datos moleculares (secuencias de ADN) y, por otro, datos morfológicos. El análisis molecular fue llevado a cabo en el Museo de Historia Natural de Nueva York, en el laboratorio del Dr. Mark Siddall.

Uno de los problemas que plantea el intentar combinar ambas fuentes de datos es que, en numerosas ocasiones, no es posible disponer del mismo grupo de taxones de los que extraer ambos tipos de información. Para la obtención de secuencias de ADN es necesario que los ejemplares se hayan fijado directamente en etanol 70-100%, sin haber pasado por la fijación en formol, paso que es necesario para la oportuna preservación del material de colecciones. Por esta razón no es posible utilizar las colecciones de museos en estudios genéticos y es preciso muestrear de nuevo con el objetivo claro de utilizar el material en estudios de filogenia molecular. Las muestras que obtuvimos para la secuenciación de ADN proceden de

diversas partes del mundo (ver Bloque III. 1) proporcionadas por varios colegas, pero una gran parte fue recolectada por el equipo de investigación de la UAM expresamente para dicho estudio. De esta manera conseguimos que el análisis molecular abarcase una gran cantidad de especies representativas de las cuatro subfamilias en Syllidae. Sin embargo, y como era de esperar, la mayoría de los géneros monotípicos poco comunes en la familia (muchos de los revisados en el Bloque II), provenientes de lugares tan dispares como Nueva Zelanda, Sudáfrica, Chile o Brasil, no pudieron ser incluidos. El análisis morfológico, sin embargo, incorporó todos los géneros de la Familia válidos hasta el momento. En este sentido es más completo porque representa el primer estudio filogenético que abarca toda la familia, aunque sólo incluyó un representante de cada género.

Desde el principio aspiramos a poder elaborar un análisis combinado de datos moleculares y morfológicos pero hemos considerado que dicho análisis se escapaba de los límites de una tesis doctoral. Hemos preferido esperar a tener más datos moleculares sobre más géneros para después incorporar los datos morfológicos basados en el análisis que aquí presentamos. De la misma manera, en este futuro estudio aplicaremos otras metodologías de inferencia filogenética como son los análisis de máxima verosimilitud y los análisis bayesianos. Pero ambos proyectos formarán parte de futuras investigaciones (ver aptdo. "Trabajos futuros").

Por último, y como consecuencia final de todos los resultados previos, hemos elaborado un cuarto bloque "**Bloque IV. Nueva propuesta de clasificación de la Familia Syllidae**". En este apartado pretendemos poner al día la clasificación de los sílidos teniendo en cuenta los avances taxonómicos y las relaciones evolutivas dentro de la familia. Este capítulo es una aproximación inicial a lo que será una futura clasificación estable de la Familia, que elaboraremos a partir del capítulo presentado en esta tesis conjuntamente con los resultados de los trabajos futuros. Muchos de estos trabajos están ya en proceso de realización y consisten en la caracterización de nuevos taxones y en la obtención de nuevas secuencias de ADN.

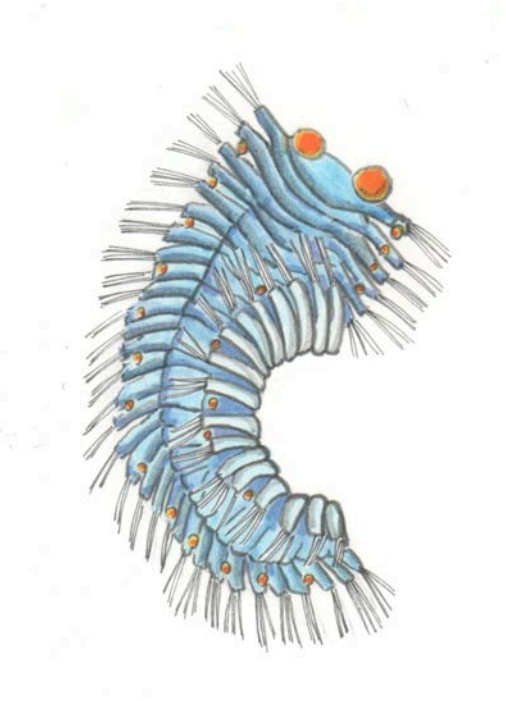
Los resultados de la tesis aparecen presentados en forma de publicaciones, de manera que cada uno de ellos mantiene su independencia como trabajo individual aunque forman parte de un estudio de mayores dimensiones con objetivos más generales. En este sentido, y para dotar

a cada trabajo de individualidad, los comienzos de cada introducción son similares ya que presentan a la Familia Syllidae y sus características. Igualmente los materiales y métodos de los trabajos eminentemente taxonómicos contienen la explicación del mismo tipo de técnicas. Existen además pequeñas diferencias de formato debido a las diferentes exigencias de cada revista científica en las que los trabajos han sido o serán publicados. Estos son los inconvenientes de la presentación de una tesis constituida por publicaciones, sin embargo, también presenta varias ventajas que son las que nos impulsaron a decantarnos por este tipo de formato. En el caso de esta tesis doctoral, supimos desde el principio que iba a ser un proyecto que se dilataría en el tiempo (por motivos profesionales de la doctoranda), así que consideramos que la publicación paulatina de los resultados agilizaría el proceso e impediría que los resultados se quedasen sin divulgar a corto plazo entre la comunidad científica. Por otro lado, este formato es el más empleado en el resto de los países europeos y en Estados Unidos, por lo que también creemos que facilitaría su divulgación internacional. El idioma de la ciencia, a nivel internacional, parece ser mayoritariamente el inglés, de ahí que prácticamente todas las revistas internacionales exijan la publicación de los resultados en esta lengua. Esto explica la combinación de español-inglés de la presente tesis.

El orden de aparición de los distintos capítulos refleja aproximadamente el orden cronológico en que han sido elaborados.

OBJETIVOS

MATERIAL Y MÉTODOS



OBJETIVOS DE LA INVESTIGACIÓN

Objectives

1. Incrementar el conocimiento taxonómico sobre la familia Syllidae en áreas poco estudiadas e investigar sobre las similitudes faunísticas entre áreas geográficamente alejadas tales como Japón, Indonesia, Panamá, estado de California (EEUU) y Líbano.

1. *To increase the taxonomic knowledge of the family Syllidae in some poorly studied areas and investigate the faunistic similarities between geographically remote regions such as Japan, Indonesia, Panama, state of California (USA) and Lebanon.*

2. Revisar los géneros y especies problemáticas, en especial varios géneros monotípicos y especies con caracteres morfológicos únicos. Estudiar los ejemplares tipo de dichos taxones y elaborar nuevas interpretaciones (cuando sea necesario) para poder establecer relaciones con el resto de las especies y géneros mejor conocidos.

2. *To revise some problematic genera and species, in particular monotypic genera and several species with unique morphological characters in the family. To study the type series of these taxa and develop new interpretations (when necessary) to establish relations with the rest of the species and the better known genera.*

3. Realizar una revisión sistemática y filogenética de toda la familia a nivel mundial. Llevar a cabo análisis cladísticos basados en datos moleculares (secuencias de ADN) y datos morfológicos obtenidos del estudio de las colecciones de sílidos estudiadas y de los géneros dudosos (objetivos 1 y 2). Discutir la monofilia de la familia, así como la monofilia de las subfamilias y de los géneros. Investigar acerca de las relaciones de parentesco entre los principales grupos dentro de la familia. Estudiar las posibles relaciones evolutivas entre los distintos procesos reproductivos y entre los diferentes sistemas de incubación.

3. *To conduct a systematic and phylogenetic review of the entire family. To perform cladistic analyses based on molecular data (DNA sequences) and morphological data obtained from the study of syllid collections and dubious genera (objectives 1 and 2). To discuss the possible monophyletic condition of the family, as well as the monophyly of the subfamilies and genera. To investigate the phylogenetic relationships within Syllidae. To study the possible evolutionary relationships between the different reproductive modes and brooding systems.*

4. Elaborar una nueva propuesta de clasificación de la familia que refleje y reúna los resultados obtenidos a lo largo de la consecución de los objetivos anteriormente mencionados.

4. *To provide a new classification for the family that reflects and summarizes the results obtained from the studies that could reach their goals above mentioned.*

MATERIAL Y MÉTODOS

1. MATERIAL

Todo el material estudiado, tanto las colecciones identificadas para esta tesis doctoral como el material comparativo de distintas instituciones, está actualmente depositado en el Museo Nacional de Ciencias Naturales de Madrid (MNCN); Zoologisches Institut und Zoologisches Museum, Universität Hamburg (ZMH); Zoologisch Museum, Universiteit van Amsterdam (ZMA); Muséum Nationale d´Histoire Naturelle, Paris (MNHN); Zoologisches Museum, Museum für Naturkunde der Humboldt-Universität, Berlin (ZMB); Australian Museum, Sydney (AM); Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt (FNS); Muzeum Przyrodnicze Wroclaw (MPW); Naturhistorisches Museum Wien (NMW); Vitenskapsmuseet, Norges Teknisk-Naturvitenskapelige Universitet, Trondheim (NTNU); Natural History Museum of London (NHML); The Smithsonian Institution, Washington (USNM); Natural History Museum of Los Angeles County (NHMLAC); South African Museum, Ciudad del Cabo (SAM); Ege Universesity, Faculty of Fisheries, Izmir (ESFM); the Kitakyushu Museum of Natural History and Human History, Fukuoka (KMNH); the Coastal Branch of Natural History Museum and Institute, Chiba (CBM); Universidad Autónoma de Nuevo León (UANL); and National Institute of Water and Atmosphere Research, Canterbury (NIWA).

2. METODOLOGÍA

2.1. Metodología de campo

Los lugares de muestreo, sustratos y profundidades donde se cogieron las muestras estudiadas están recogidos en las secciones de “Material y métodos” o “Material and methods” de los distintos capítulos (ver Bloques I-III). Las muestras, una vez obtenidas fueron filtradas y tratadas con formol al 10% como fijador y etanol al 70% como conservante

(a excepción de las muestras tomadas para el análisis filogenético molecular que se fijaron directamente en etanol 70-100%).

2.2. Metodología de laboratorio

Para la identificación de los ejemplares se utilizó una lupa binocular Olympus SZ30, un microscopio óptico Olympus CH30 y un microscopio óptico Nikon 104 provisto del sistema de contraste de fases interferencial de Nomarsky, con mayor capacidad de resolución, que permite el análisis de estructuras de especial interés. La iconografía se realizó a escala con la ayuda de una cámara clara Nikon y un ocular milimetrado acoplables al microscopio con sistema interferencial de Nomarsky. Las fotografías al microscopio electrónico de barrido se llevaron a cabo en el SIDI (Servicio Interdepartamental de Investigación) de la Universidad Autónoma de Madrid. Se siguió protocolo específico de deshidratación de los ejemplares seleccionados que consiste en su introducción paulatina en una secuencia de diluciones de acetona, con una concentración de acetona gradualmente mayor. Una vez deshidratados, los ejemplares fueron llevados al punto crítico en dióxido de carbono y a continuación fueron cubiertos por una fina capa de oro para su posterior observación con un microscopio electrónico Phillips XL-30. Finalmente, se realizaron preparaciones permanentes en las que se usó gel de glicerina para la fijación de los ejemplares seleccionados.

La identificación de la fauna de poliquetos se realizó con la ayuda de claves y descripciones que aparecen tanto en los textos clásicos sobre diferentes áreas geográficas, como en monografías y revisiones específicas sobre familias y géneros, además de diversas publicaciones donde se recogen descripciones de especies nuevas, redescripciones o nuevas citas. Todos estos trabajos están recogidos en los apartados de “Referencias” o “*References*” correspondientes a cada capítulo.

2.3. Metodología filogenética

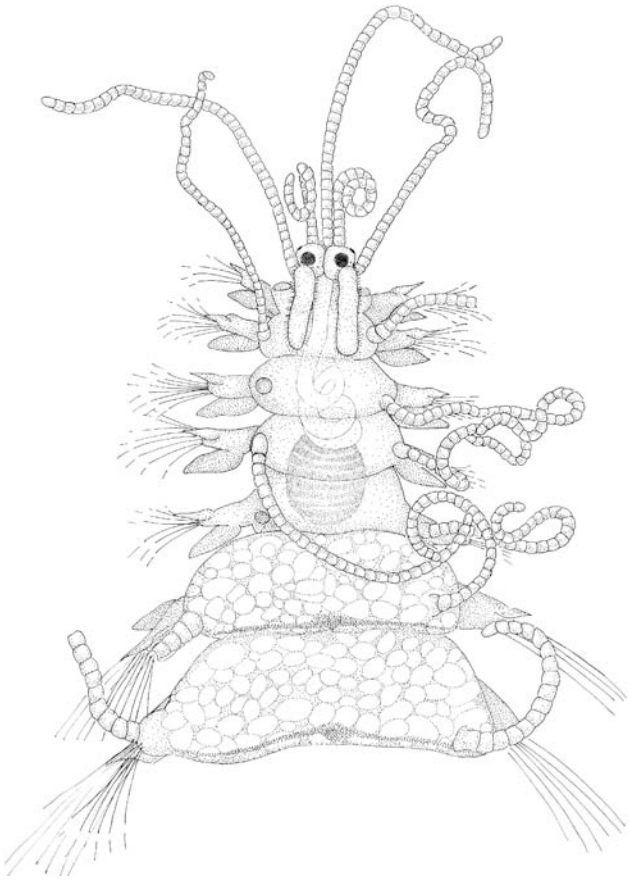
a) Para la realización del análisis filogenético basado en datos moleculares se seleccionaron ejemplares que, debidamente fijados en alcohol 70-100%, representaban a las cuatro subfamilias. A continuación, se extrajo y se purificó el ADN de cada ejemplar y se

procedió a la amplificación de las secuencias de los genes seleccionados usando "*primers"* universales (oligonucleótidos cebadores que sirven de punto de anclaje para la ADN polimerasa) (ver "Material and methods" del Bloque III.1). Posteriormente los genes se secuenciaron y finalmente se alinearon las secuencias con ayuda de programas informáticos como Clustal X version 1.83 (Thompson *et al.*, 1997) y el alineamiento se revisó con la ayuda del programa MacClade (Maddison and Maddison, 2001). El análisis de parsimonia se llevó a cabo con el programa PAUP* 4.0b10 (Swofford, 2002) en combinación con PAUPRat "Paup*implementation of the parsimony ratchet" (Nixon, 1999), betaversion 1 (Sikes y Lewis, 2001), y con el programa TNT (Goloboff *et al.*, 2004). Se realizaron 3000 réplicas. Todos los caracteres fueron considerados de igual peso y no aditivos. Se calcularon valores de soporte de Bremen (Bremer, 1988) y Symmetric Resampling frequencies (Goloboff *et al.*, 2003).

b) Para la realización del análisis filogenético basado en datos morfológicos se procedió de la siguiente manera: En primer lugar, se seleccionaron las especies que iban a ser utilizadas como taxones terminales. Muchas de ellas fueron las especies tipo, pero se seleccionaron otras especies del género cuando el conocimiento de su morfología y/o de su reproducción era más detallado. La información sobre los caracteres se extrajo del estudio directo de las series tipo de cada especie, cuando fue posible, de material de diversas partes del mundo (ver metodología del primer apartado) y de fuentes bibliográficas (descripciones originales, posteriores revisiones y trabajos sobre reproducción). Para la codificación de caracteres se siguió el método C (Pleijel, 1995) que consiste en codificar las estructuras complejas mediante varios caracteres, de los cuales el primero incorpora la información de ausencia/presencia de la estructura. Los caracteres fueron considerados como no aditivos y todos de igual peso. El análisis de parsimonia se llevó a cabo usando los mismos programas y parámetros que el molecular (ver apartado a) a excepción de los valores de soporte de Symmetric resampling que fueron substituidos por la prueba de Jackniffe (Farris *et al.*, 1996).

BLOQUE I

ESTUDIO TAXONÓMICO DE LA FAMILIA SYLLIDAE



1. Sílidos intersticiales (Syllidae: Polychaeta) del Parque Nacional de Coiba (Pacífico, Panamá). Aguado, M.T. & G. San Martín. 2006. *Revista de Biología Tropical*.

2. Two New Species of Syllidae (Annelida: Polychaeta) from Japan. Aguado, M.T., San Martín, G. & E. Nishi. 2006. *Scientia Marina*.

3. Syllidae (Polychaeta) from Japan with the descriptions of three new species. Aguado, M.T., San Martín & Nishi. Submitted. *Systematics and Biology*.

4. A new species of *Opisthosyllis* (Polychaeta: Syllidae) from California (U.S.A.). Aguado, M.T, San Martín, G. & Nygren, A. 2005. *Zootaxa*.

5. Syllidae (Annelida: Polychaeta) from Indonesia collected in the Siboga (1899-1900) and Snellius II (1984) expeditions. Aguado, M.T., San Martín, G. & Ten Hove, H. In press. *Zootaxa*.

6. Syllidae (Polychaeta) from Lebanon with two new reports for the Mediterranean Sea. Aguado, M.T. & San Martín, G. 2007. *Cahiers de Biologie Marine*.

Sílidos (Syllidae: Polychaeta) del Parque Nacional de Coiba (Pacífico, Panamá)

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Abstract: Syllids (Syllidae: Polychaeta) from Coiba National Park (Pacific of Panama). During a study carried out on soft bottoms from Coiba National Park (Panama), 218 specimens of syllids (Annelida: Polychaeta) belonging to 19 interstitial species have been identified. Two species are new reports for the Pacific Ocean, *Exogone (Exogone) arenosa* Perkins, 1981 and *Streptosyllis websteri* Southern, 1914; five are new for Panama, *E. (E.) dispar* (Webster, 1879); *E. (E.) longicornis* Westheide, 1974; *Salvatoria mediodentata* (Westheide, 1974); *Pionosyllis heterocirrata* (Hartmann-Schröder, 1959) and *Syllis glarearia* (Westheide, 1974). A characteristic not mentioned in the original description is herein reported for *E. (E.) longicornis*: the presence of triangular subterminal processes in the spiniger-like compound chaetae of chaetiger one. Specimens of the species *Syllis botosaneanui* Hartmann-Schröder, 1973 harboring inside embryos of various stages of development have been found; this is the first report for this species as viviparous. Lastly, one specimen of the genus *Syllis* has been found that is mainly characterized by its long pharynx, two dorsal prostomial lobes, and compound chaetae with short blades and long spinulation. Because we consider that one specimen is not sufficient to describe a new species we refer it as *Syllis* sp. Rev. Biol. Trop. 54 (3): 725-743. Epub 2006 Sept. 29.

Key words: polychaeta, Syllidae, Coiba, Pacific, Panama, viviparity.

El Parque Nacional de Coiba es uno de los parques nacionales con mayor superficie marina protegida del mundo (216.543 ha). Se encuentra situado a 150 millas náuticas de la costa Pacífica de Panamá, y está formado por un archipiélago; la mayor de sus islas es la que le da nombre al Parque. La descripción del medio marino del Parque está recogida en López *et al*. (1997, 2002), San Martín (2000, 2001) y San Martín *et al*. (1997a, b).

Como resultado de las expediciones llevadas a cabo desde 1996 por el equipo del laboratorio de Biología Marina e Invertebrados de la Universidad Autónoma de Madrid, la criptofauna coralina del Parque y, en particular, la fauna de poliquetos han sido estudiados en varios trabajos (San Martín *et al*. 1997a, b, Capa *et al*. 2001a, b, c). Los tres trabajos últimos se refieren específicamente a la familia Syllidae de la criptofauna coralina del Parque. Es por ello que el presente trabajo se ha centrado en las especies de sílidos identificados en muestras de arena, lo cual permite conseguir un inventario más completo de esta familia en Coiba.

Algunos trabajos anteriores a 1997 en los que se estudian los poliquetos del Pacífico panameño entre ellos, la familia Syllidae pueden consultarse en Capa *et al.* (2001a, b, c).

MATERIALES Y MÉTODOS

El material procede de cinco muestras tomadas en sustratos blandos en tres estaciones

del Parque Nacional de Coiba durante el mes de Septiembre de 1998. Las muestras tomadas en Mali Rock (7º39' N, 81º41'40" W) y Granito de Oro (7º35'30" N, 81º42'30" W) son de arenas gruesas submareales, procedentes de la destrucción de coral (a 10 m y 0.5 m de profundidad, respectivamente). Las tres restantes son intermareales, de arena media a gruesa y fueron tomadas en la playa de El Gambute (7º37'25" N, 81º43' W) a tres alturas diferentes (nivel de pleamar, nivel intermedio de marea y nivel de bajamar).

Las muestras se obtuvieron introduciendo en el sedimento un tubo de PVC de 1 litro de capacidad. Posteriormente fueron filtradas utilizando un tamiz con luz de malla de 0.1 mm de diámetro, fijadas en formol (10%) y preservadas en etanol (70%) tras la identificación de los ejemplares. Para la identificación se ha utilizado una lupa binocular Olympus SZ30, un microscopio óptico Olympus CH30 y un microscopio óptico Nikon 104 provisto del sistema de contraste de fases interferencial de Nomarsky. Para la realización de los dibujos se ha empleado una cámara clara Nikon y un ocular milimetrado. Las fotografías al microscopio electrónico de barrido (MEB) se llevaron a cabo en el SIDI (Servicio Interdepartamental de Investigación) de la Universidad Autónoma de Madrid. Los ejemplares están depositados en el Museo Nacional de Ciencias Naturales de Madrid y en la colección de Poliquetos del Laboratorio de Biología Marina e Invertebrados de la Universidad Autónoma de Madrid.

RESULTADOS

Han sido identificados 218 ejemplares de sílidos, pertenecientes a nueve géneros y 19 especies, de las cuales dos son nuevas citas para el Pacífico: *Exogone arenosa* Perkins, 1981 y *Streptosyllis websteri* Southern, 1914. Otras cinco son nuevas citas para Panamá: *E. dispar* (Webster, 1879); *E. longicornis* Westheide, 1974; *Salvatoria mediodentata* (Westheide, 1974); *Pionosyllis heterocirrata* (Hartmann-Schröder, 1959) y *Syllis glarearia* (Westheide, 1974). Para *E. longicornis* se detalla una nueva característica no mencionada en descripciones previas, la posesión de proyecciones terminales en los mangos de las pseudoespiníferas del primer setígero. Se describe la especie *Syllis botosaneaunui* Hartmann-Schröder, 1973 como especie vivípara y, por último, se describe la especie *Syllis* sp., que probablemente sea una especie no descrita hasta el momento, pero al tener un sólo ejemplar preferimos no darle un nuevo nombre.

Subfamilia Exogoninae
Langerhans, 1879
Género *Brania*
Quatrefages, 1866
Brania sp.

Material examinado: Granito de Oro (un ejemplar).

Discusión: El ejemplar está incompleto y en mal estado de conservación, por lo que no puede ser determinado hasta nivel de especie.

Género *Exogone*
Örsted, 1845
Subgénero *Exogone*
Örsted, 1845
E. (Exogone) arenosa
Perkins, 1981

E. arenosa: Perkins, 1981: 1094-107, Fig. 5 g-j, 6.
E. (Exogone) arenosa: San Martín, 1991: 736.

Material examinado: Granito de Oro (50 ejemplares).

Discusión: *E. arenosa, E. lourei* Berkeley & Berkeley, 1938 y *E. pseudolourei* San Martín, 1991 son especies muy similares, todas ellas presentes en el Caribe, y cuyas sedas compuestas son muy parecidas, pues siempre presentan una notoria expansión triangular en la región subterminal del mango. *E. arenosa* se caracteriza por tener un proventrículo largo (30 filas de células musculares, siete segmentos) y una espina en la punta de las sedas

simples dorsales; sin embargo, *E. lourei* y *E. pseudolourei* tienen un proventrículo corto (aproximadamente 20 filas de células musculares, 2.5 segmentos) y no presentan espina en las sedas simples dorsales. *E. pseudolourei* se diferencia de *E. lourei* en la forma y grosor de la seda simple dorsal.

Perkins (1981) y San Martín (1991) diferencian estas especies principalmente por la longitud del proventrículo. San Martín (1991) describe ejemplares de Cuba de *E. arenosa* con y sin espina en la seda simple dorsal y siendo ésta, cuando existe, muy variable en tamaño. Atendiendo a este criterio, los ejemplares de Coiba poseen todos ellos un proventrículo largo por lo que son considerados como *E. arenosa*, aunque algunos presentan una espina más reducida que la descrita por Perkins (1981), y algunos carecen de ella.

Distribución: Atlántico (Florida, Cuba, islas Canarias) Pacífico (Panamá, primera cita).

Exogone (Exogone) breviantennata
Hartmann-Schröder, 1959

E. breviantennata: Hartmann-Schröder 1959: 125, Fig. 75-78; Zottoli & Long 2000: 502, Fig. 1-5.
E. (Exogone) breviantennata: San Martín 1991: 730; 2005: 141-142, Fig. 81 e, 89 a-i; Núñez *et al.* 1992: 47, Fig. 3; López *et al*. 1997: 63.

Material examinado: Granito de Oro (seis ejemplares).

Distribución: Pacífico (Canadá, México, Ecuador, Galápagos, Japón, Australia y Panamá) Atlántico (Venezuela, Cuba, Panamá y Canarias) Índico (Australia).

Exogone (Exogone) dispar
(Webster, 1879)

E. dispar: Westheide 1974: 106, Fig. 48 a-h, 49 a-d; Perkins 1981: 1090; Uebelacker 1984: 43, Fig. 30-36.
E. (Exogone) dispar: San Martín 1991: 729; 2005: 137-138, Fig. 81 f, 85 a-g.

Material examinado: Granito de Oro (tres ejemplares).

Distribución: Mediterráneo Atlántico (Norte América, Golfo de México, Cuba) Pacífico (Galápagos, Australia y Panamá, primera cita).

E. (Exogone) longicornis
Westheide, 1974, Fig. 1

E. longicornis: Westheide, 1974: 309-313, Fig. 54-55.

Material examinado: Granito de Oro (13 ejemplares).

Material adicional: Dos ejemplares de Galápagos: Serie tipo, Westheide, 1974. Dos ejemplares de Australia: Isla de Beacon, 113º47' E 28º25.5' S, coral muerto, -12 m (un ejemplar) (AM W26666); Isla de Wallaby, 113º40.9' E 28º27.9' S en *Posidonia australis*, -2 m (un ejemplar) (AM W26667).

Descripción: Ejemplar de mayor tamaño de 33 setígeros, 2.9 mm de longitud y 0.2 mm de anchura, a nivel del proventrículo. Prostomio semicircular con dos pares de ojos dispuestos en trapecio, el par anterior bilobulado. Tres antenas insertas entre el par anterior de ojos, la central considerablemente más larga, cinco a seis veces más que las laterales, estrechándose distalmente, llegando a parecer articulada. Palpos robustos, más largos que el prostomio. Segmento bucal tapado parcialmente por el prostomio, provisto de un par de cirros tentaculares ovoides, de menor tamaño que el resto de los cirros dorsales, y cirros ventrales ovalados, ligeramente más pequeños que los dorsales (Fig. 1A). Pseudoespinígera del primer setígero con el mango engrosado en su parte distal, con prolongación subtriangular provista en su cara superior de espinas muy finas; artejo de 13.2 µm de longitud, finamente espinulado y con el extremo bífido (Fig. 1B). En el primer setígero, aparecen también cinco sedas falcígeras de mango densamente espinulado y con artejos, de 4.6 µm de longitud, provistos de un gran diente secundario y un diente principal mucho más corto y fino que el

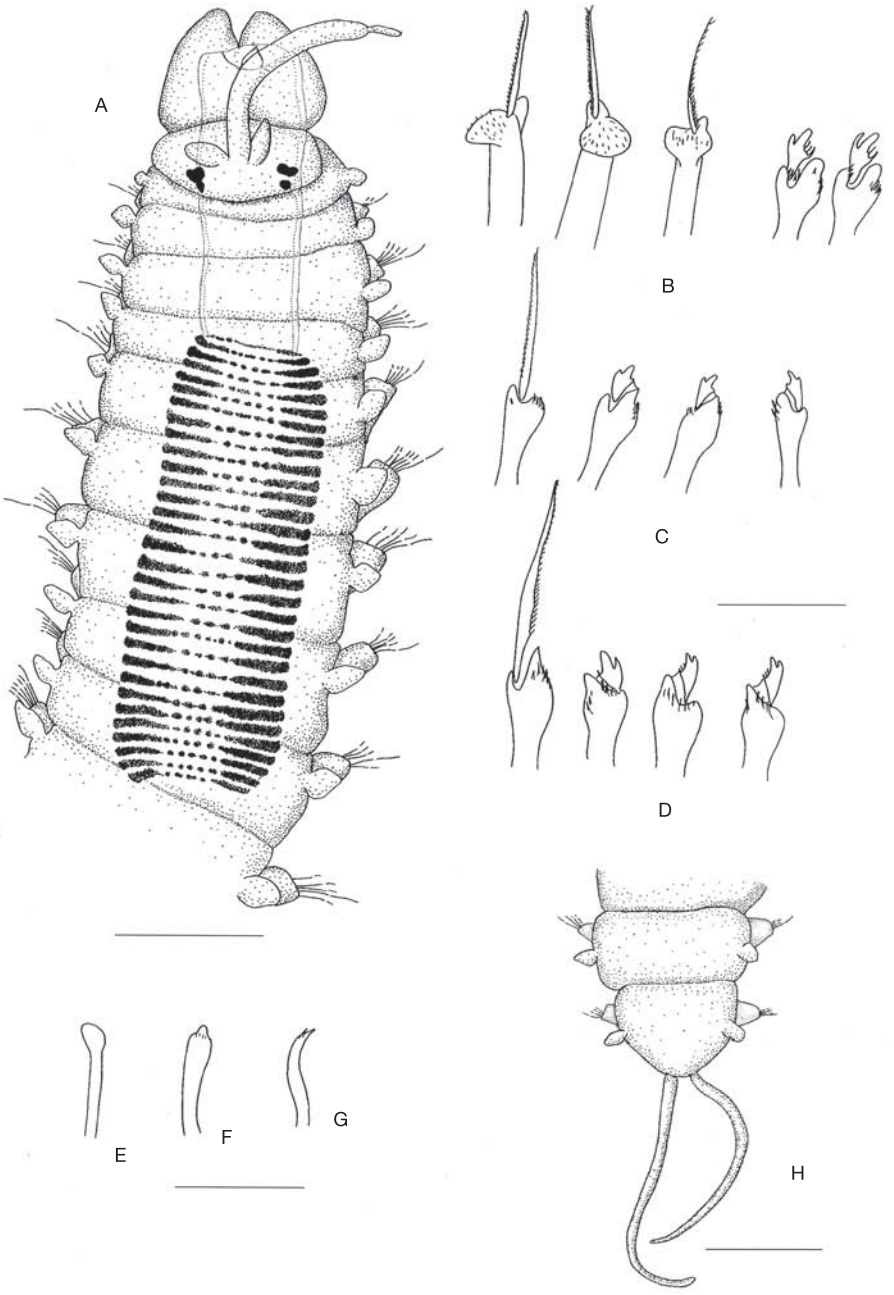

Fig. 1. *Exogone (Exogone) longicornis*. A. Parte anterior, vista dorsal; B. Sedas compuestas, primer setígero; C. Sedas compuestas, setígero medio; D. Sedas compuestas, setígero posterior; E. Acícula, setígero medio; F. Seda simple dorsal, setígero posterior; G. Seda simple ventral, setígero posterior; H. Pigidio, vista dorsal. Escala A, H. 0.16 mm; B-G. 20 µm. B-E. (modificado de San Martín 2005).

Fig. 1. *Exogone (Exogone) longicornis*. A. Anterior part, dorsal view; B. Compound chaetae, first chaetiger; C. Compound chaetae, medium chaetiger; D. Compound chaetae, posterior chaetiger; E. Acicula, médium chaetiger; F. Dorsal, simple chaeta, posterior chaetiger; G. Ventral, simple chaeta, posterior chaetiger; H. Pygidium, dorsal view. Scale A, H. 0.16 mm; B-G. 20 µm. B-E. (after San Martín 2005).

anterior y 2-3 espinas largas y delgadas (Fig. 1B). Siguientes segmentos, con el mango de la pseudoespinígera no engrosado en ninguno de los casos. Segundo setígero con una seda pseudoespinígera ligeramente bífida, carácter que se va perdiendo en los siguientes setígeros. Pseudospinígeras de los segmentos anteriores de mayor longitud que la del primer setígero (29.7 µm) y 5-6 falcígeras similares a las del primer setígero, pero con espinas más cortas (Fig. 1C). Las pseudoespinígeras decrecen en longitud en los segmentos posteriores (14.5 µm) y en las falcígeras no se observan las espinas. Seda dorsal simple con un engrosamiento espinulado subdistal, a partir del primer setígero. Seda simple ventral, en los segmentos posteriores, curvada y bidentada con el diente secundario más desarrollado que el principal (Fig. 1G). Parápodos con una sola acícula acabada en un engrosamiento (Fig. 1E). Pigidio con un par de cirros anales largos (Fig. 1H). Faringe larga que ocupa, aproximadamente cinco setígeros, con un grueso diente en su parte anterior. Proventrículo largo de unas 30 filas de células musculares, llegando a ocupar cuatro o cinco setígeros (Fig. 1A). Varios ejemplares tienen la parte posterior cargada de huevos, en el interior de los segmentos comprendidos entre el 14 y el 23. También se ha encontrado un ejemplar con un embrión lateral.

Discusión: Han sido revisados dos ejemplares de Galápagos pertenecientes a la serie tipo que, al igual que en los ejemplares de Coiba y otros procedentes de Australia, poseen los mangos de la pseudoespinígeras del primer setígero modificados con procesos triangulares subterminales, característica que no se recoge en la descripción original.

Distribución: Pacífico (Islas Galápagos, Australia y Panamá, primera cita).

Exogone (Exogone) lourei
Berkeley & Berkeley, 1938

E. (Exogone) lourei: Berkeley & Berkeley, 1938: 44-47, Fig. 6-10; Banse 1972: 200, Fig. 5 a-d; Perkins 1981: 1092; Uebelacker 1984: 39-41, Fig. 33-34 (en parte); San Martín 1991: 735; 2005: 129-130, Fig. 78 a-j; Núñez *et al*. 1992: 46-47; Kudenov & Harris 1995: 15-17, Fig. 1.3; Capa *et al*. 2001c: 623.

Material examinado: Mali Rock (2 ejemplares).

Material adicional: Material de fondos duros de Coiba (T2F97).

Discusión: Los ejemplares coinciden con la descripción original y con el material revisado de fondos duros de Coiba (Capa *et al*. 2001c).

Distribución: Pacífico (desde Canadá hasta Panamá), Atlántico (Islas de Cabo Verde y Canarias), Caribe (Golfo de México y Cuba), Índico (Australia).

Género *Salvatoria*
Mc Intosh, 1885

Siguiendo los criterios de San Martín (2005), las especies descritas o citadas dentro del género *Grubeosyllis* Verrill, 1900, pasan a ser incluidas en el género *Salvatoria*. Las dos especies de este género encontradas en este trabajo constituyen una nueva combinación.

Salvatoria heterocirra
(Rioja,1941), n. comb.

Brania heterocirra: Rioja, 1941: 700, pl. 3, Fig. 11-13; Westheide 1974: 83, Fig. 38, 39.
Grubeosyllis heterocirra: López *et al.* 1997: 63; Capa *et al.* 2001c: 624.

Material examinado: Granito de Oro (dos ejemplares).

Distribución: Pacífico (Islas Galápagos, México y Panamá), Caribe (Cuba).

Salvatoria mediodentata
(Westheide, 1974), n. comb

Brania mediodentata: Westheide, 1974: 93-94, Fig. 42 a-c, 43; Russell 1991: 52-54, Fig. 1.
Grubeosyllis mediodentata: Díaz-Castañeda & San Martín 2001: 710-712, Fig. 2-4.

Material examinado: Granito de Oro (29 ejemplares).

Distribución: Caribe (Cuba, Belice) Pacífico (Islas Galápagos, México y Panamá, nueva cita).

Subfamilia Eusyllinae
Malaquin, 1893
Género *Odontosyllis*
Claparède, 1963
Odontosyllis fulgurans
Audouin & Milne Edward, 1834

O. fulgurans: Pettibone 1963: 122, Fig. 35 c; Imajima & Hartman 1964: 113; San Martín 1984: 93-97, Fig. 14; 2003: 104-106, Fig. 46, 47; Capa *et al.* 2001c: 622.

Material examinado: Mali Rock (un ejemplar).

Distribución: Mediterráneo, Atlántico oriental, Pacífico (Japón, Islas Galápagos, Panamá).

Género *Pionosyllis*
Malmgren, 1867
Pionosyllis heterocirrata
(Hartmann-Schröder, 1959)

Eusyllis heterocirrata: Hartmann-Schröder, 1959: 118, Fig. 64-66; 1974: 45.
P. heterocirrata: Hartmann-Schröder 1992: 224-226, Fig. 11-15.

Material examinado: Mali Rock (tres ejemplares); Granito de Oro (siete ejemplares).

Distribución: Atlántico (Isla de Ascensión), Índico (Tanzania, Sudáfrica), Pacífico (El Salvador y Panamá, primera cita).

Pionosyllis sp.

Pionosyllis sp.: Gardiner 1976: 137.
Pionosyllis cf. *uraga*: Day 1973: 33, Fig. 4 km.
P. uraga (Non Imajima, 1966): Perkins 1981: 1108.

Material examinado: Mali Rock (un ejemplar).

Material adicional: Ejemplares del Caribe: Florida, Golfo de México, Cuba.

Discusión: Esta especie está actualmente en proceso de descripción dentro de un trabajo monográfico de revisión del género *Pionosyllis* (San Martín *et al.*, en prep.).

Distribución: Atlántico (desde Carolina del Norte hasta Venezuela), Pacífico (Panamá).

Género *Paraehlersia*
San Martín, 2003
Paraehlersia articulata
Kudenov & Harris, 1995, n. comb

Pionosyllis articulata: Kudenov & Harris 1995: 55-58, Fig. 1.20; Capa *et al.* 2001c: 622-623.

Material examinado: Granito de Oro (cuatro ejemplares).

Discusión: Los caracteres de esta especie coinciden con la diagnosis del género *Paraehlersia* de San Martín (2003), por lo que transferimos esta especie a dicho género tras comprobar la existencia de bandas ciliares y de papila subcirral, característica propia de este género. Los ejemplares coinciden con la descripción de Kudenov & Harris (1995), aunque son de mayor tamaño. Los autores describen los cirros dorsales lisos y los dos últimos tercios de las antenas articulados y los ejemplares estudiados tienen los cirros de los primeros setígeros articulados, pero aproximadamente a partir del 4º-5º setígero se vuelven lisos y sus antenas son articuladas prácticamente desde la base. Las diferencias en el grado de articulación de los cirros dorsales anteriores están relacionadas con el tamaño de los ejemplares, siendo totalmente lisos en los más pequeños y más fuertemente articulados en los de mayor tamaño. Estas diferencias ya habían sido relacionadas por San Martín (2003) con el tamaño de los ejemplares para la especie *P. ferrugina* (Langerhans, 1881).

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Distribución: Pacífico (California, Panamá).

Género *Streptosyllis*
Webster & Benedict, 1884
Streptosyllis websteri
Southern, 1914. Fig. 2

S. websteri: Southern, 1914: 26-28**,** pl. 2, Fig. 3S-F; Fauvel 1923: 282, Fig.107; Campoy 1982: 312; Parapar *et al.* 1994: 94, Fig. 1F-G; Brito *et al.* 2000: 607-609, Fig. 3.
Streptosyllis pettiboneae: Perkins 1981: 1143, Fig. 27 A-F, 28 A-I.

Material examinado: Granito de Oro (un ejemplar).

Descripción: Ejemplar de 2.89 mm de longitud, 0.19 mm de anchura a nivel del proventrículo (sin contabilizar apéndices) y 34 setígeros. Prostomio ovalado, dos pares de ojos dispuestos en trapecio y dos manchas oculares anteriores. Palpos pequeños no visibles dorsalmente. Una antena lateral presente, ovoide, lisa, inarticulada insertada al nivel del primer par de ojos anteriores; inserción de la central al nivel del segundo par de ojos posterior. Segmento tentacular estrecho con dos pares de cirros tentaculares inarticulados largos de más del doble de la longitud del resto de los cirros dorsales. Cirros dorsales cortos y esféricos. Cirros ventrales largos, más del doble de largos que los lóbulos parapodiales, gruesos en la base y digitiformes hacia el extremo; algunos en la región media y posterior del cuerpo, con tres o cuatro pseudoartejos con inclusiones doradas brillantes en su interior de difícil visualización. Acículas gruesas, engrosadas distalmente. En los segmentos segundo al quinto fuertemente engrosadas (Fig. 2A-E). Seda simple dorsal en todos los setígeros, en los primeros setígeros (hasta el quinto) son curvadas distalmente y con fuerte serración en el borde convexo (Fig. 2G), en el resto de los segmentos sin curvatura tan marcada, con fuerte serración en su borde convexo y capuchón transparente recubriendo el extremo distal de la seda que acaba en dos pequeñas púas (Fig. 2I). En los cinco primeros setígeros hay dos sedas compuestas con artejo falcígero largo (19 µm), bidentado, con filo dentado y articulación subhemigonfa; y seis sedas compuestas con el mango grueso, artejo corto (6-12 µm), en algunos casos llegando a parecer bidentado, articulación engrosada, homogonfa y con algunas espinas (Fig. 2H). A partir del sexto setígero, falcígeras bidentadas, en número de seis a ocho, con articulación heterogonfa, codo anterior de la articulación provisto de un grueso diente subdistal, de artejos irregularmente dentados y en gradación dorsoventral en longitud (24 µm el más largo y 16 µm el más corto, podio medio) (Fig. 2J). Tres cirros anales, dos de ellos cortos. Faringe gruesa, inerme, más corta que el proventrículo. Proventrículo ocupando 4-5 setígeros, de 45-50 filas de células musculares.

Discusión: El ejemplar coincide con la descripción y dibujos de *S. pettiboneae* Perkins, 1981 de Florida, que es considerado por Brito *et al.* (2000) como sinónima de *S. websteri* ya que ambas tienen acículas engrosadas y sedas compuestas modificadas en los setígeros dos a seis (aunque presenten alguna diferencia morfológica en los artejos), así como el mismo tipo de sedas compuestas a partir del setígero siete. Los tipos de *S. pettiboneae* han sido examinados por Brito *et al.* (2000) y señalan que coinciden con sus ejemplares de Canarias y que se corresponden con la descripción original de Southern (1914).

Distribución: Atlántico (desde Irlanda hasta las Islas Canarias, Golfo de México), Mediterráneo, Pacífico (Panamá, primera cita).

Género *Syllides*
Örsted, 1845
Syllides sp.

Material examinado: Granito de Oro (un ejemplar).

Discusión: Un único ejemplar en mal estado y de identificación dudosa.

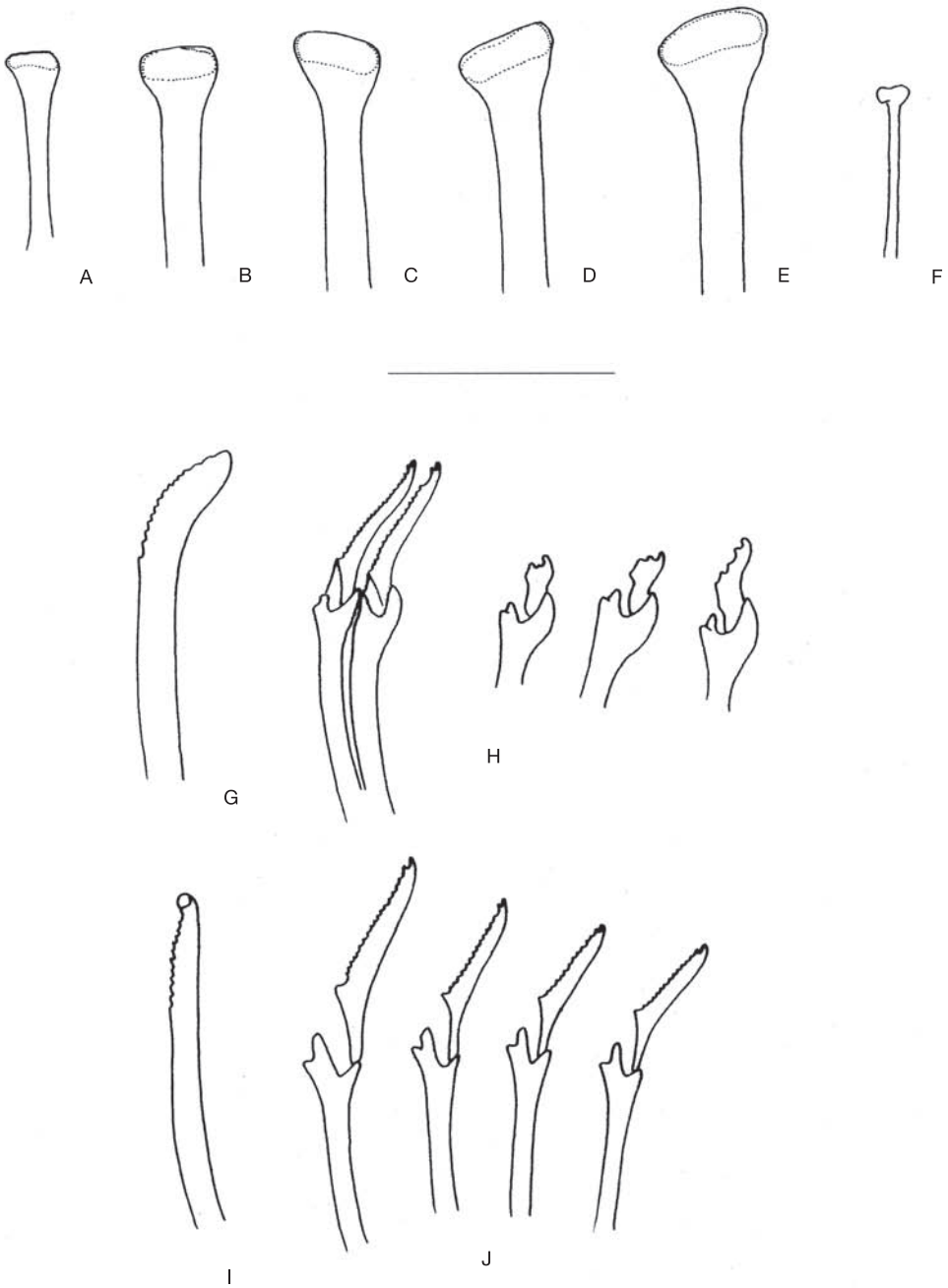

Fig. 2. *Streptosyllis websteri.* A. Acícula, primer setígero; B. Acícula, segundo setígero; C. Acícula, tercer setígero; D. Acícula, cuarto setígero; E. Acícula, quinto setígero; F. Acícula, a partir del sexto setígero; G. Seda simple dorsal, setígero anterior; H. Sedas compuestas, setígero anterior; I. Seda simple ventral, setígero posterior. Escala: A-J: 20 µm.

Fig. 2. *Streptosyllis websteri.* A. Acicula, first chaetiger; B. Acicula, second chaetiger; C. Acicula, third chaetiger; D. Acicula, fourth chaetiger; E. Acicula, fifth chaetiger; F. Acicula, from six chaetiger to the end of the body; G. Dorsal, simple chaeta, anterior chaetiger; H. Compound chaetae, anterior chaetiger; I. Ventral, simple chaeta, posterior chaetiger: Scale: A-J: 20 µm.

Género *Syllis*
Savigny, 1818
Syllis beneliahuae
(Campoy & Alquezar, 1982)

Langerhansia beneliahui: Campoy & Alquézar, 1982: 124-125, Fig. 3 a-p.
Syllis beneliahui: San Martín 1992: 183, Fig. 1 k-m.
Typosyllis beneliahuae: Licher 1999: 47-48, Fig. 22.
S. beneliahuae: Capa *et al.* 2001a: 107.

Material examinado: El Gambute (nivel de bajamar) (un ejemplar).

Distribución: Mediterráneo occidental, Atlántico oriental, Caribe, Pacífico (Panamá).

Syllis botosaneanui
Hartmann-Schröder, 1973
Fig. 3-5

Typosyllis (Langerhansia) botosaneanui: Hartmann-Schröder, 1973: 90-93, Fig. 5-8; 1977: 55-56; 1980: 391; 1992: 223.
Typosyllis botosaneanui: Licher, 1999: 68-70, Fig. 31.
Syllis botosaneanui: Capa *et al*. 2001a: 107.
Syllis garciai: San Martín, 1992: 180-181, Fig. 5 a-d. Non *S. garciai* Campoy, 1982.

Material examinado: Mali Rock (siete ejemplares); Granito de Oro (33 ejemplares); El Gambute (nivel intermedio de marea) (44 ejemplares); El Gambute (nivel de bajamar) (tres ejemplares).

Descripción: Uno de los ejemplares de mayor tamaño, de la muestra de Granito de Oro, tiene juveniles en su interior y se encuentra en buen estado de conservación (Fig. 3A), de 4.3 mm de longitud, 0.27 de anchura a nivel del proventrículo, y 46 setígeros. Cuerpo grande, largo y cilíndrico. Prostomio semicircular, con cuatro ojos dispuestos en trapecio abierto hacia la parte anterior y dos manchas oculares anteriores (justo por delante de las antenas laterales) (Fig. 3A). Tres antenas; la central más larga que las laterales, inserta entre los ojos posteriores, con 14 artejos; laterales con nueve. Palpos robustos, triangulares, de tamaño igual o mayor que el prostomio (Fig. 5A). Dos pares de cirros tentaculares, los dorsales con 12 artejos, los ventrales con nueve. Cirros dorsales del primer setígero con unos 15 artejos; los de los dos setígeros siguientes son más cortos (siete artejos); a continuación, alternando largos (8-10 artejos) y cortos (6-7 artejos). Dos cirros anales similares a los dorsales (7-15 artejos), y un corto apéndice anal impar inarticulado (Fig. 3B). Artejos de los apéndices con inclusiones espirales en su interior. Podios cónicos, cirros ventrales digitiformes, de longitud igual o menor que el lóbulo parapodial. Podios anteriores normalmente con dos sedas pseudoespinígeras, a veces una, presentes desde el primer setígero, con artejos de 66 µm de longitud, unidentados o finamente bidentados con espinas largas y finas, y con cinco falcígeras con artejos bidentados, en gradación dorsoventral, tres más largas, de 16-18 µm, con larga espinulación, que no llega a sobrepasar el nivel del diente secundario; y dos cortas, de 12-13 µm, con espinulación más corta (Fig. 4B, 5E). Podios medios con una pseudoespinígera similar a las anteriores pero más larga (96 µm), con un diente proximal difícil de ver (Fig. 4C, 5C-D) y cuatro falcígeras dispuestas en parejas de 20 µm y 96-120 µm de longitud respectivamente, fuertemente bidentadas; los artejos de mayor longitud con espinulación desarrollada y larga (Fig. 4C). Últimos podios de disposición similar, con una pseudoespinígera unidentada, de 89 µm de longitud, y cuatro falcígeras fuertemente bidentadas, tres de ellas de 17-18 µm con espinulación más corta que las de los podios medios y anteriores y una de 14 µm con espinulación también más corta y mango algo engrosado (Fig. 4D). En algunos ejemplares de mayor tamaño (16-24 mm de longitud y 113-134 setígeros), las pseudoespinígeras son considerablemente más cortas que las de los segmentos medios (aproximadamente menos de la mitad). Una acícula en cada parápodo con un ensanchamiento subdistal y una punta oblicua afilada. Una seda simple dorsal gruesa, bífida en el extremo, y muy finamente espinulada en su borde interno (Fig.

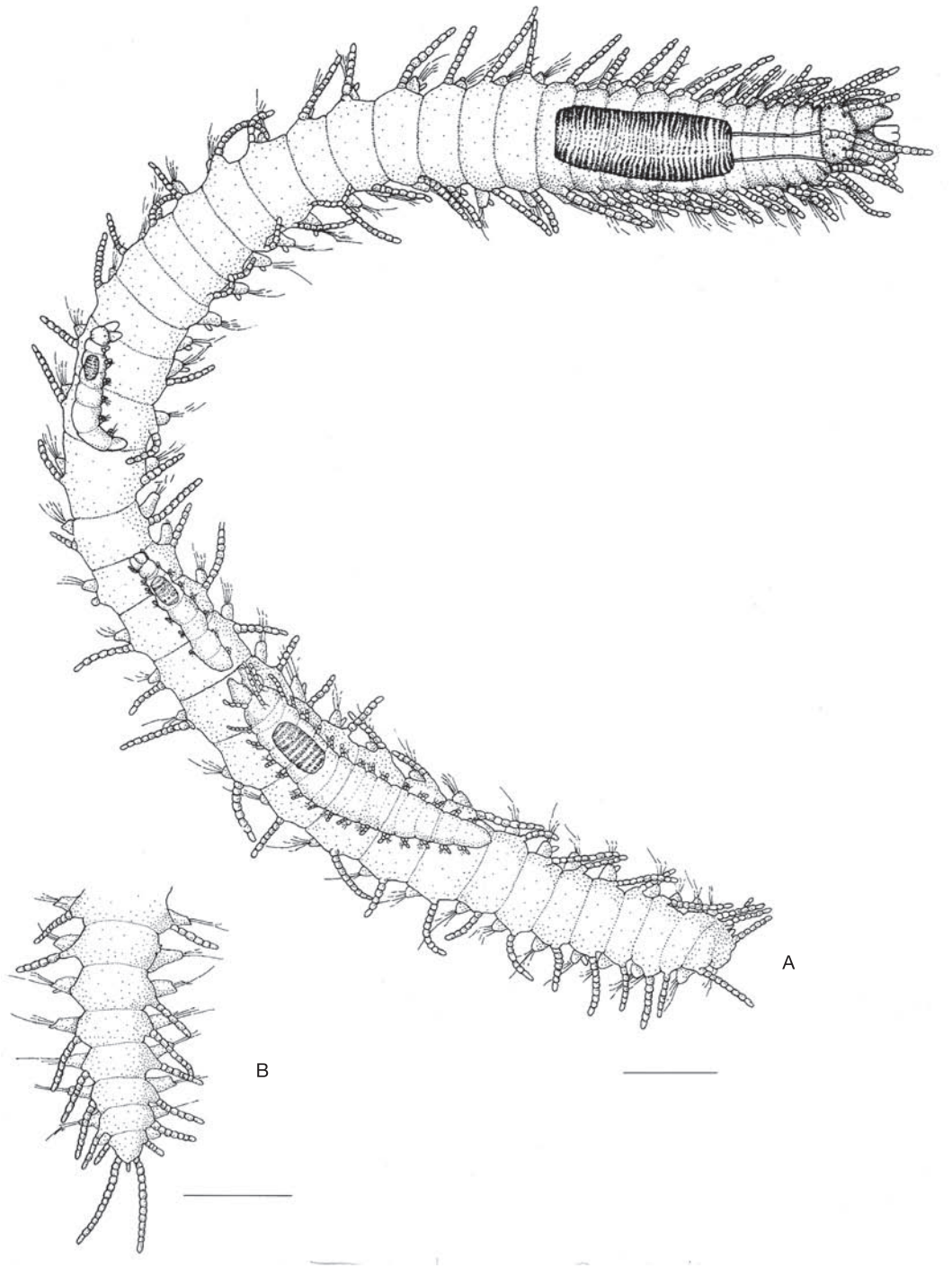

Fig. 3. *Syllis botosaneanui*. A. Ejemplar completo con embriones en su interior; B, Pigidio, vista dorsal. Escala A, B: 2 mm.

Fig. 3. *Syllis botosaneanui*. A, Complete specimen with embryos inside; B, Pygidium, dorsal view. Scale A, B: 2 mm.

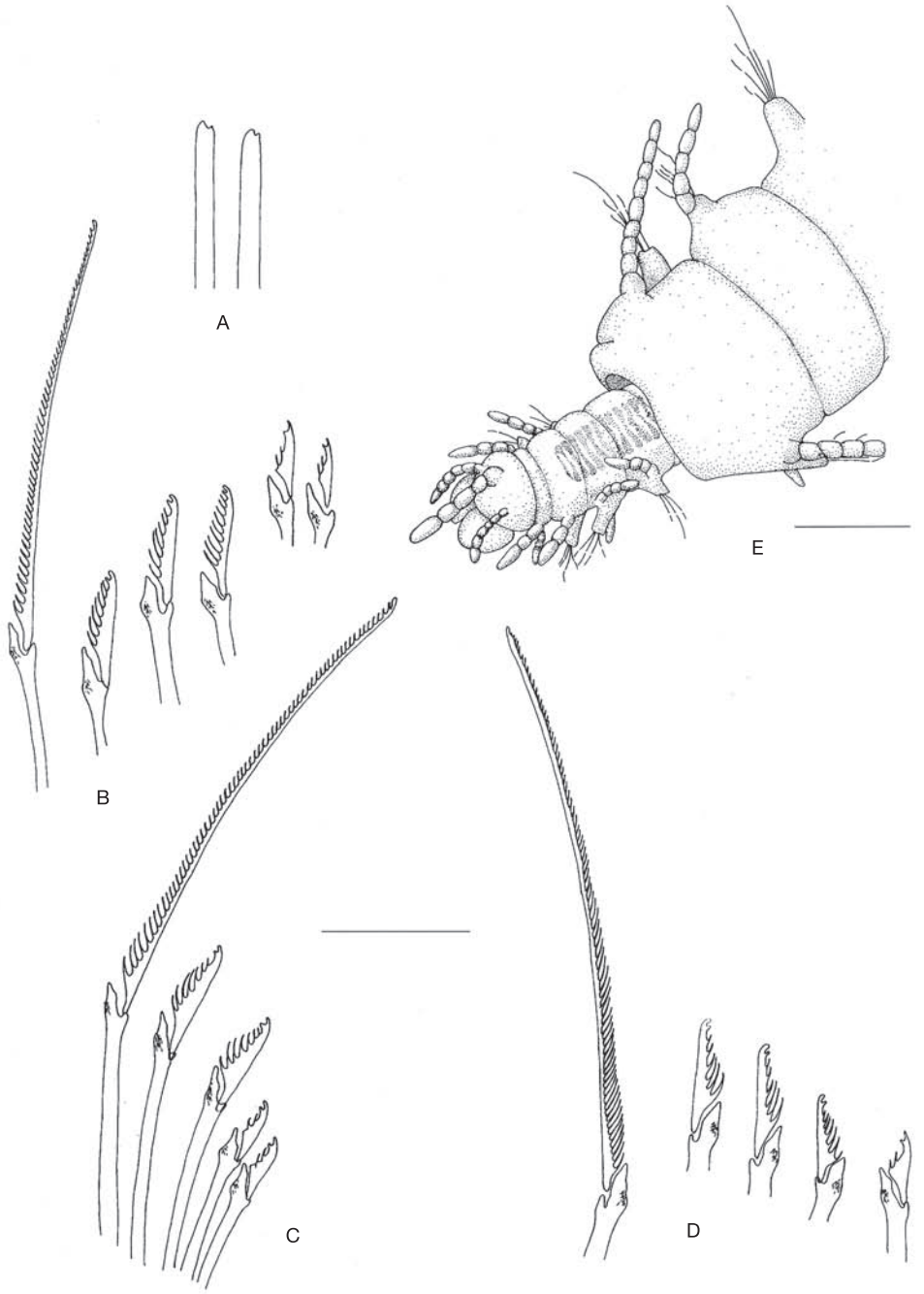

Fig. 4. *Syllis botosaneanui*. A, Sedas simples dorsales, setígero medio; B, Sedas compuestas, setígero anterior; C, Sedas compuestas, setígero medio; D, Sedas compuestas, setígero posterior; E, Embrión saliendo del cuerpo partido de la madre. Escala A-D: 20 µm; E: 97.5 µm.

Fig. 4. *Syllis botosaneanui*. A. Dorsal simple chaetae, midbody chaetiger; B. Compound chaetae, anterior chaetiger; C. Compound chaetae, midbody chaetiger; D. Compound chaetae, posterior chaetiger; E. Embryo protruding from mother's cut body. Scale A-D: 20 µm; E: 97.5 µm.

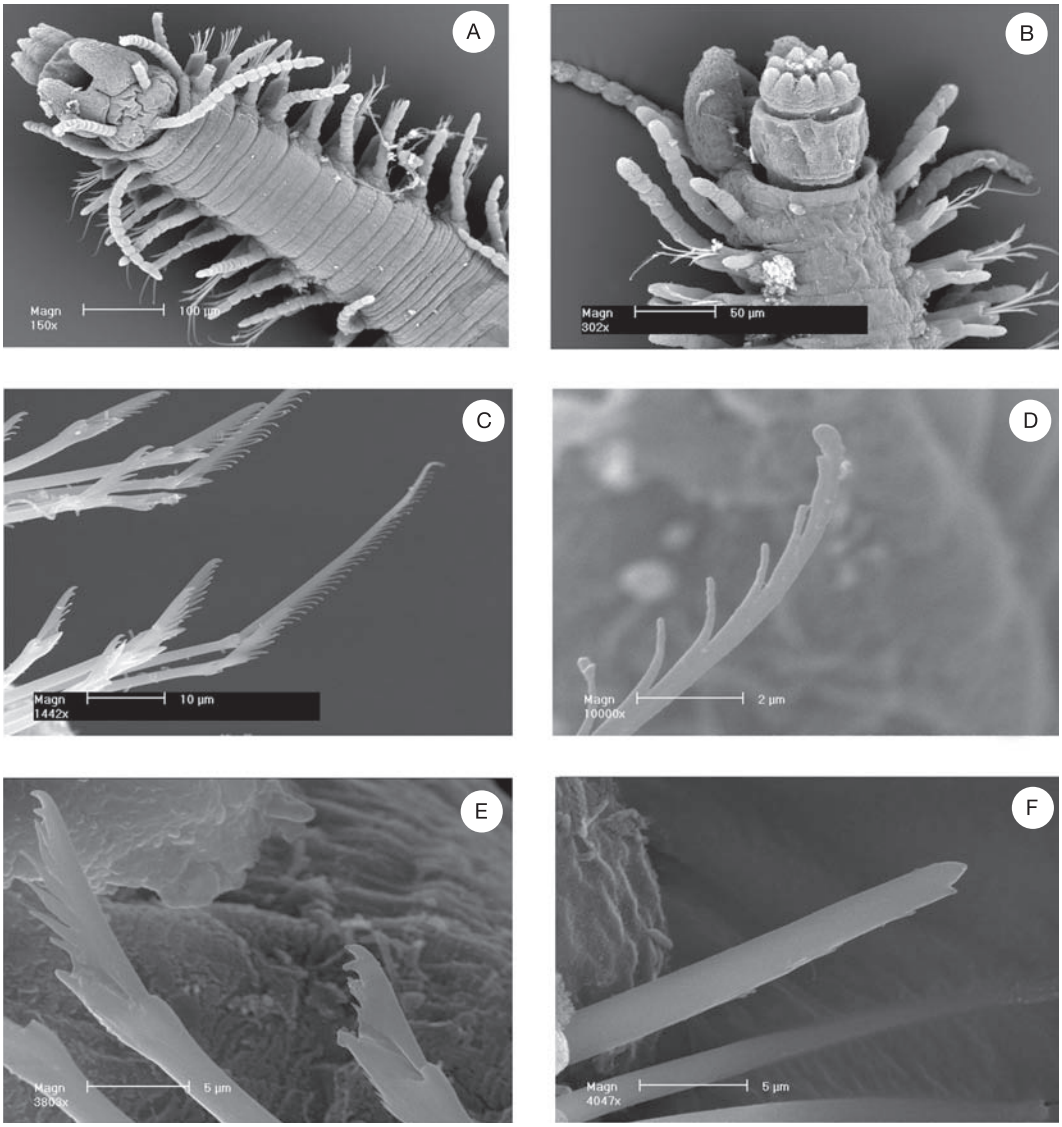

Fig. 5. *Syllis* sp. 1. Fotografías al microscopio electrónico de barrido (MEB). A. Parte anterior, vista dorsal; B. Parte anterior, vista ventral, probóscide evaginada; C. Sedas compuestas, setígero medio; D. Parte distal, seda compuesta pseudoespinígera, setígero medio; E. Seda falcígera inferior, setígero medio; F. Seda falcígera media, setígero medio; G. Seda simple dorsal, setígero posterior.

Fig. 5. *Syllis* sp. 1. Scanning electron micrographs (SEM). A. Anterior part, dorsal view; B. Anterior part, ventral view, evaginated proboscis; C. Compound chaetae, midbody chaetiger; D. Distal part, pseudospiniger chaeta, midbody chaetiger; E. Inferior falciger chaeta, midbody chaetiger; F. Middle falciger chaeta, midbody chaetiger; G. Dorsal simple chaeta, posterior chaetiger.

4A, 5F), y una seda simple ventral bidentada y finamente espinulada. Faringe cilíndrica, larga y generalmente muy oscura, con la embocadura rodeada de 10 grandes papilas (Fig. 5B) y provista de un grueso diente en su comienzo. Proventrículo de tamaño similar a la faringe con unas 33-40 filas musculares, que ocupa seis segmentos (Fig. 3A).

Discusión: A pesar de corresponder a una misma época del año, se ha encontrado diferencias de tamaño entre los ejemplares de las distintas muestras, siendo los ejemplares de Granito de Oro los de menor longitud del cuerpo y número de setígeros. Doce ejemplares de esta muestra (de 2-4 mm de longitud), presentan en su interior embriones en diverso estado de desarrollo (Fig. 1A). Los ejemplares de Mali Rock son mucho mayores, llegando a alcanzar una longitud de 24 y 16 mm; el más pequeño tiene un juvenil en su interior. Los ejemplares de El Gambute son de tamaño intermedio (8-11 mm), más delgados que los de Granito de Oro, y ninguno de ellos presenta juveniles.

De un total de 83 ejemplares revisados, 13 presentan uno o varios embriones en su cavidad celómica, en su mayoría, en la mitad posterior del cuerpo. En ninguno de los casos aparecen emergiendo del cuerpo del progenitor; uno de los ejemplares muestra en su parte final al embrión con la mitad de su cuerpo fuera debido a que probablemente se partiese justo por la zona donde se aloja la cría (Fig. 2E). Habitualmente también se observan huevos esféricos de color oscuro (uno de los ejemplares con cinco embriones y tres huevos). Normalmente, cuando aparecen varias crías en un ejemplar, éstas se encuentran en diferente estado de desarrollo. En ocasiones sólo se distinguen los palpos y los parápodos sin sedas y en otros casos se observa perfectamente su anatomía. Los embriones aparecen orientados indistintamente hacia la parte posterior o anterior del cuerpo del adulto.

S. botosaneanui y *S. garciai* Campoy, 1982 son dos especies muy similares, ambas citadas en Coiba por Capa *et al*. (2001a), que se diferencian principalmente por la longitud de la espinulación de los artejos de las sedas falcígeras, siendo más larga en *S. garciai* donde llega a sobrepasar el nivel del diente secundario. En los ejemplares de Coiba la espinulación de los artejos es muy larga y fina, de mayor longitud que la dibujada por Hartmann-Schröder (1973) y Licher (1999) pero no llega a sobrepasar el nivel del diente secundario. Por último, *S. botosaneanui* es una especie de fondos blandos, calificada como intersticial (Hartmann-Schröder 1980, Licher 1999), por lo que el hábitat coincide con el de nuestros ejemplares. Los ejemplares son determinados como *S. botosaneanui* siendo ésta la primera referencia de la especie como vivípara.

El viviparismo, como estrategia reproductora en sílidos, ha sido citada para *Syllis vivipara* Krohn, 1869; *Syllis nepiotoca* Caullery & Mesnil, 1916; *Syllis incisa* Augener, 1929; *Syllis parturiens* (Haswell, 1920); *Exogone parahomoseta mediterranea* San Martín, 1984 y *Exogone hebes* Webster & Benedict, 1884; y más recientemente para *Dentatisyllis mangalis* Russell, 1995 y *Dentatisyllis mortoni* Ding *et al.*, 1998 (Krohn 1869, Goodrich 1900, Caullery y Mesnil 1916, Ben-Eliahu 1977, Pocklington y Hutcheson 1983, San Martín 1984, Russell 1995, Ding *et al.* 1998, Franke 1999). El viviparismo, que aparece indistintamente en diferentes subfamilias (Syllinae y Exogoninae), podría interpretarse como una adaptación al medio intersticial, más que una estrategia propia de los ciclos vitales de determinados géneros (Ding *et al*.1998).

Distribución: Caribe (Cuba), Índico, Atlántico occidental (Isla Ascensión), Pacífico (Panamá).

Syllis glarearia
(Westheide, 1974), n. comb.

Typosyllis glarearia Westheide, 1974: 55-58; Licher 1999: 175-177, Fig. 78.

Siguiendo los criterios de San Martín (1992, 2003), consideramos las especies descritas dentro de *Typosyllis* Langerhans, 1879, como pertenecientes a *Syllis*, por lo que esta especie constituye una nueva combinación.

Material examinado: Mali Rock (tres ejemplares); Granito de Oro (un ejemplar).

Distribución: Pacífico (Islas Galápagos y Panamá, primera cita).

Syllis magna
(Westheide, 1974)

Ehlersia rosea magna Westheide, 1974: 41-45, Fig. 17, 18.
Typosyllis magna: Licher 1999: 49, Fig. 23.
Syllis magna: Capa *et al.* 2001a: 112.

Material examinado: Granito de Oro (1 ejemplar).

Distribución: Pacífico (Islas Galápagos, Panamá).

Syllis sp.
Fig. 6

Material examinado: Mali Rock (1 ejemplar: MNCN 16.01/8875)

Descripción: Único ejemplar de 14 mm de longitud y 0.5 mm de anchura a nivel del proventrículo y 64 setígeros. Cuerpo largo, cilíndrico. Prostomio subpentagonal con extremo redondeado y dos lóbulos dorsales sobre los que se encuentran los ojos, dispuestos en trapecio abierto anteriormente. Tres antenas, la central más larga que las laterales, con 17 artejos, inserta entre ambos lóbulos al nivel del par de ojos posterior; antenas laterales, con 15 artejos, insertas anteriormente, en el comienzo de los lóbulos. Dos palpos robustos, más largos que el prostomio (Fig. 6A). Dos pares de cirros tentaculares, los dorsales con 13 artejos y los ventrales con nueve. Cirros dorsales alternando irregularmente entre largos y cortos, los largos con alrededor de 30 artejos y los cortos con 10-12 artejos, antenas y cirros dorsales delgados y frágiles. Cirros anales ausentes. Podios cónicos, cirros ventrales digitiformes más largos que el parápodo (Fig. 6E); cada parápodo con siete u ocho sedas compuestas heterogonfas con artejos en ligera gradación dorsoventral en longitud. Artejos cortos bidentados, diente subdistal muy pequeño, con espinas largas en la base, anchas en su comienzo, finas y dirigidas hacia arriba en el extremo distal. En podios anteriores, las tres sedas compuestas más dorsales con artejos de espinulación gruesa y patente que miden 15 µm de longitud; las dos o tres sedas siguientes con artejos ligeramente menores, 11-13 µm, con fina espinulación y las dos últimas sedas más ventrales con artejos de menor tamaño sin espinulación, con diente subdistal y 9 µm de longitud (Fig. 6B). Forma y número de artejos similares en podios medios y posteriores, pero aumentando progresivamente de tamaño hacia la parte posterior. En los segmentos medios los tres artejos dorsales miden 16 µm, los dos o tres siguientes 15 µm y los dos ventrales 13 µm; en los podios posteriores, los tres artejos dorsales miden 17 µm, los dos o tres medios 16 µm y los dos ventrales 15 µm. Seda simple dorsal en podios posteriores con una pequeña escotadura en su extremo distal (Fig. 6F). Seda simple ventral ausente. Parápodos anteriores y medios con cuatro acículas delgadas con punta oblicua (Fig. 6C); los posteriores con dos acículas de punta oblicua con un engrosamiento subdistal, más gruesas que las anteriores (Fig. 6D). Faringe cilíndrica extremadamente larga, a través de 12-13 segmentos, parcialmente evertida y de color más oscuro que el resto del cuerpo, embocadura sin papilas, con un diente cónico en su comienzo. Proventrículo muy grande, unas 47-50 filas de células musculares, ocupando ocho segmentos (Fig. 6A).

Discusión: *Syllis* sp. se caracteriza por presentar sedas compuestas con artejos cortos, triangulares, tenuemente bidentados, provistos de espinulación larga y gruesa en la base, dirigida hacia arriba, y que se va haciendo progresivamente más corta hacia el extremo del artejo, disminuyendo el tamaño de las espinas cuanto más ventral sea la seda, llegando los artejos a ser totalmente lisos en las más ventrales, junto con una faringe muy larga y un proventrículo aproximadamente la mitad de la longitud de la faringe. *Syllis glarearia* (Westheide, 1974), presenta sedas con artejos más largos, con el diente proximal mayor que el distal, y con las espinas de las sedas largas en posición distal. Unas diferencias similares se pueden apreciar con respecto a *Syllis lutea* (Hartmann-Schröder, 1960), del mar Rojo, y *S. jorgei* San Martín & López, 2000, del Mediterráneo occidental. *Syllis adamanteus* (Treadwell, 1914), del Pacífico Norte, *Syllis*

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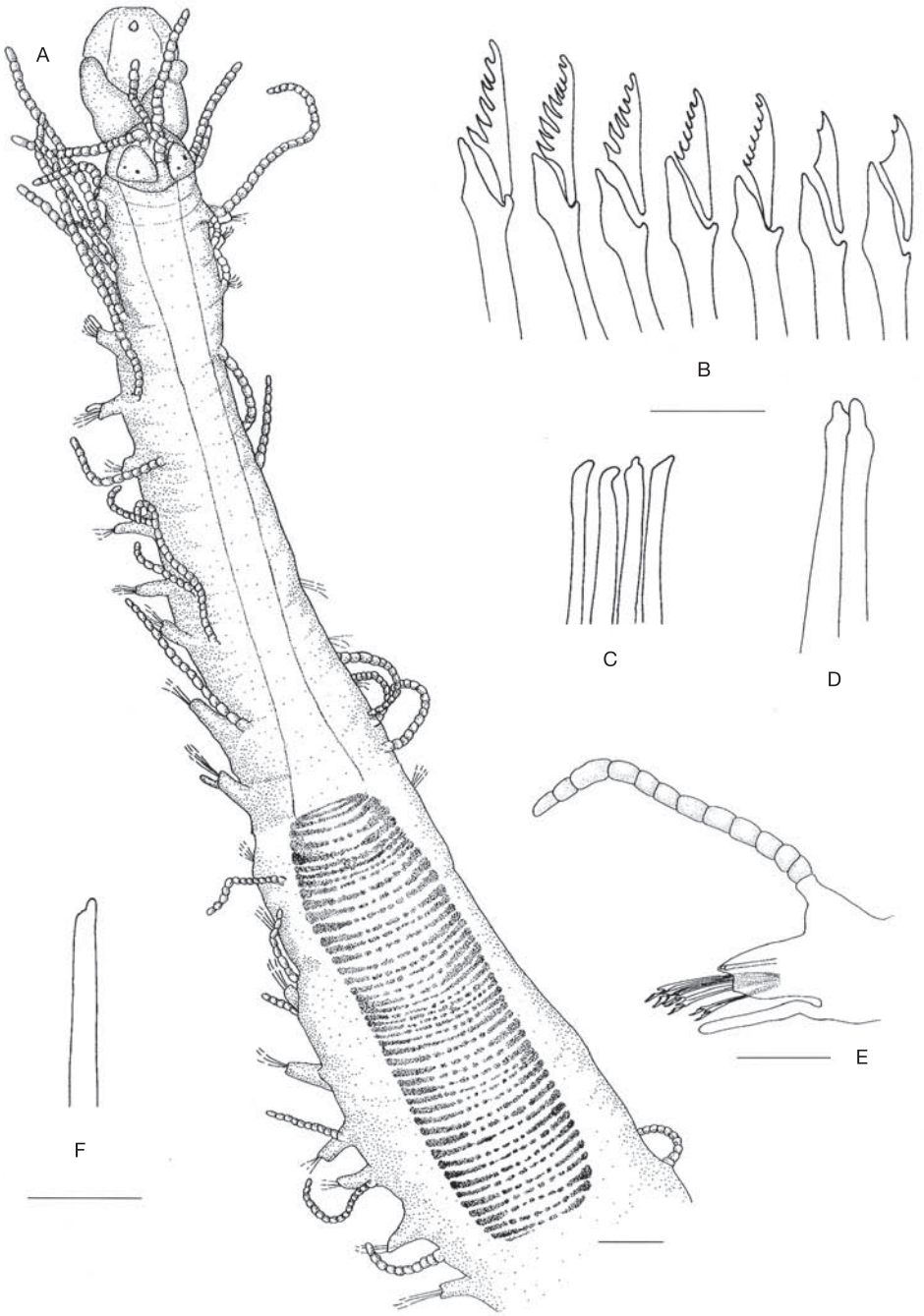

Fig. 6. *Syllis* sp. A. Parte anterior, vista dorsal; B. Sedas compuestas, setígero anterior; C. Acículas, setígero anterior; D. Acículas, setígero posterior; E. Parápodo derecho, segmento medio, vista anterior; F. Seda simple dorsal, setígero medio. Escala A: 97.5 µm; B-D, F: 10 µm; E: 48 µm.

Fig. 6. *Syllis* sp. A. Anterior part, dorsal view; B. Compound chaetae, anterior chaetiger; C. Aciculae, anterior chaetiger; D. Aciculae, posterior chaetiger; E. Right parapodium, midbody chaetiger, anterior view; F. Dorsal simple chaeta, midbody chaetiger. Scale A: 97.5 µm; B-H: 10 µm; I: 48 µm.

dayi (Hartmann-Schröder, 1974), del Oeste de África, *Syllis magdalena* (Wesenberg-Lund, 1962), del Sur de Sudamérica, *Syllis pectinans* Haswell, 1920, de Australia, también citado en el Parque Nacional Coiba, y *Syllis anoculata* (Hartmann-Schröder, 1962), de Chile, son especies similares, también con sedas compuestas de artejos cortos, provistos de espinulación moderadamente larga, pero en todos los casos la sedas son unidentadas, mientras que en *Syllis* sp. son claramente bidentadas. Quizás, la especie más similar es *Syllis licheri* Ravara, San Martín & Moreira, 2004, de las costas atlánticas de la península Ibérica, pues los artejos de las sedas son también cortos y triangulares, pero en esta especie, hay sedas bidentadas y otras unidentadas, la espinulación de los artejos es siempre mucho más corta, y una acícula muy gruesa que sobresale de los lóbulos parapodiales, lo que no sucede en *Syllis* sp. Ninguna de las especies similares descritas (Haswell 1920, Wesenberg-Lund 1962, Hartmann-Schröder 1973, 1974, 1991, Licher 1999, San Martín y López 2000, San Martín 2003, Ravara, 2004) presentan las características de *Syllis* sp. pero, al tener un solo ejemplar, preferimos no nombrarla como nueva hasta encontrar más ejemplares que corroboren las características de este espécimen.

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RESUMEN

Durante un estudio sobre la fauna marina del Parque Nacional de Coiba (Panamá) se identificaron 281 ejemplares de sílidos (Annelida: Polychaeta) intersticiales pertenecientes a 19 especies. Dos son nuevas citas para el Pacífico, *Exogone (Exogone) arenosa* Perkins, 1981 y *Streptosyllis websteri* Southern, 1914; cinco son nuevas citas para Panamá, *E. (E.) dispar* (Webster, 1879), *E. (E.) longicornis* Westheide, 1974, *Salvatoria mediodentata* (Westheide, 1974); *Pionosyllis heterocirrata* (Hartmann-Schröder, 1959) y *Syllis glarearia* (Westheide, 1974). Se describe un caracter no presente en la descripción original de *E. Longicornis*, la presencia de procesos triangulares subterminales en la primera pseudospinígera. Se describen ejemplares de la especie *Syllis botosaneanui* Hartmann-Schröder, 1973 con embriones en diverso estado de desarrollo en su interior, por lo que se trata de la primera referencia de esta especie como vivípara. Por último, se describe un ejemplar de *Syllis* sp., que se caracteriza fundamentalmente por la posesión de una larga faringe, dos lóbulos prostomiales dorsales y por sus sedas compuestas de artejos cortos y larga espinulación. Estas características diferencian a *Syllis* sp. de cualquier especie del género pero no se describe como especie nueva por disponerse únicamente de un solo ejemplar.

Palabras clave: Polychaeta, Syllidae, Coiba, Pacífico, Panamá, viviparismo.

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Two new species of Syllidae (Polychaeta) from Japan

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SUMMARY: Two new species of Japanese Syllidae (Polychaeta) belonging to the genera *Haplosyllis* Langerhans, 1879 and *Syllis* Lamarck, 1818 are described. *Haplosyllis crassicirrata* n. sp. is characterized by its distinctly spindle-shaped thick dorsal cirri, with yellow granular inclusions, two unequal simple chaetae per parapodium, and the shape of the chaetae. *Syllis marugani* n. sp. is characterized by its distinct orange colour (in ethanol preserved specimens), long and broad dorsal cirri, compound chaetae having robust shafts in the posterior part of the body, and short blades strongly bidentate.

Keywords: *Haplosyllis*, *Syllis*, Syllidae, polychaetes, taxonomy, systematics.

RESUMEN: DOS NUEVAS ESPECIES DE SYLLIDAE (POLYCHAETA) DE JAPÓN. – Se describen dos nuevas especies de sílidos (Polychaeta) japoneses pertenecientes a los géneros *Haplosyllis* Langerhans, 1879 y *Syllis* Lamarck, 1818. *Haplosyllis crassicirrata* n. sp. se caracteriza principalmente por poseer cirros anchos, fusiformes, con inclusions granulares de color amarillo en su interior, dos sedas simples desiguales por parápodo y por la forma de estas sedas. *Syllis marugani* n. sp. se caracteriza principalmente por poseer color naranja (en ejemplares preservados en etanol), cirros dorsales largos y anchos, y sedas compuestas con mangos robustos y angulosos en la parte posterior del cuerpo, y artejos cortos fuertemente bidentados.

Palabras clave: *Haplosyllis, Syllis,* Syllidae, poliquetos, taxonomía, sistemática.

INTRODUCTION

The family Syllidae is one of the most diverse families comprising about 667 valid species and 55 genera (San Martín, 2003). It is a widely distributed group found from the intertidal zone to the abyssal plains all over the world (Pleijel, 2001; Glasby, 2000); yet they are more diversified and abundant in shallow waters (San Martín, 2003).

Even though several studies and extensive monographs deal with the diversity of the syllids in Japan, complete knowledge of the group remains elusive. The earliest works on Japanese polychaetes including Syllidae species are those of Marenzeller (1879), McIntosh (1879), Moore (1903) and Izuka (1912), the latter being a compilation of the previous works. Subsequent studies were carried out by Fauvel (1934, 1936), although only the first one treated syllids specifically. Subsequently, Utinomi (1956) studied syllid commensals on gorgonaceans, and Imajima and Hartman (1964) published a monograph on the polychaetous annelids of Japan that included the family Syllidae. Two years later, Imajima (1966a-f) published a series of six papers on the different subfamilies of Syllidae in which he described several new taxa. More recent works are those of Ohwada (1988), Imajima (1997, 2003) and San Martín and Nishi (2003). Syllids have been studied in Korea by Wui Lee and Jo Rho (1994), in China and surrounding areas by Jing and Baoling

(1991), Fan *et al*. (1993), Ding and Westheide (1994, 1997), and Ding *et al*. (1998), and along the eastern coast of Russia (López *et al*., 2001).

MATERIAL AND METHODS

The specimens were found in two intertidal samples (M1 and M15), where M1 was collected on algal substrata in Manazuru Peninsula (35º10'22''N, 130º41'E) and M15 collected on rocky shore in Yoshio, Katsuura City, Boso Peninsula (35º08'10''N, 140º18'16''E).

The samples were fixed in 10% formaldehyde-seawater solution and preserved in 70% alcohol. For identification, an Olympus SZ30 stereomicroscope and Olympus CH30 microscope were used. Drawings were made using a drawing tube on a Nikon Optiphot microscope equipped with interference contrast optics (Nomarski). Width of specimens reported was always measured at the level of the proventricle and excluding parapodia.

The type-series are deposited in the Museo Nacional de Ciencias Naturales de Madrid (MNCNM-CSIC), Spain. Description of the morphology of the largest chaetae of *Haplosyllis crassicirrata* n. sp. follows the terminology proposed by Martín *et al*. (2003) for species of the genus *Haplosyllis* (see Fig. 2A).

RESULTS

Haplosyllis crassicirrata n. sp.
(Figs. 1, 2)

Material examined: M15. Holotype MNCN 16.01/10135; Paratypes (2) MNCN 16.01/10136.
Comparative material examined: *Haplosyllis basticola* Sardá, Ávila and Valerie (MNCN 16.01/8439).

Etymology. The name makes reference to the thick dorsal cirri.

Description. Length of holotype 2.1 mm and width 0.3 mm, for 16 chaetigers (Fig. 1A). First paratype is incomplete, length 2.4 mm and width 0.3 mm, for 15 chaetigers and second paratype complete, length 1.6 mm and width 0.2 mm for 14 chaetigers. Body short, transparent and slightly yellowish. Prostomium broader than long, rectangular to oval with two pairs of small eyes in a trapezoidal arrangement. Palps broad, fused basally, slightly longer than prostomium. Median antenna inserted on middle of prostomium, long, with 23-25 articles, approximately three times longer than lateral antennae. Lateral antennae inserted on anterior part of prostomium, with 8-12 articles, slightly longer than prostomium and palps together (Fig. 1A). Peristomium shorter than following segments (Figs. 1A,B). Dorsal tentacular cirri with 11-15 articles, ventral ones with 5 articles. Dorsal cirri of 1st chaetiger longer than tentacular ones, with 20-27 articles. Subsequent cirri considerably shorter, with no more than 6 articles, without alternation in length, and considerably broader, thick, spindle-shaped, brightly and intensely coloured yellow by granular material inside. Posterior dorsal cirri decreasing in length (Fig. 1A,B). Ventral cirri oval and short, not extending beyond tips of parapodia. Two unequal simple chaetae per parapodium, one distinctly longer and wider than the other (Fig. 1E). In largest chaeta (Fig. 2A and caption), base of main fang (BMF; 2.9 µm) longer than distance between main fang upper insertion and mid-joining point between teeth (MJ; 1.3 µm); length of main fang (LMF; 1.2 µm) smaller than chaetal width (SW; 2.6 µm); upper side of main fang (US; 3.2 µm), clearly longer than lower side (LS; 1.3 µm). Two teeth at the tip of the chaeta, distal one clearly smaller, with a narrow angle between them. Denticles on the upper side of the main fang not seen. Small chaeta (Fig. 2B) with fang not as curved as large chaeta; both teeth at tip of chaeta similar in size and with a narrow angle between them. Denticles not present on upper side of fang. One acicula inside each parapodium, slightly leaning to one side at tip (Fig. 1D). Pygidium conical, in paratype 16.01/10136 with two short, pyriform anal cirri, similar in length to dorsal cirri, but not articulated (Figs. 1A,B). Pharynx short, extending through 2-3 segments, narrower than proventricle, provided with 10 papillae (Fig. 1C) and one small, conical distal tooth (Fig. 1B). Proventricle short and barrel-shaped, similar in length to pharynx, extending through 2 segments (Figs. 1A,B).

Remarks. This new species is characterized by its small size; long and slender antennae, tentacular cirri and long dorsal cirri of 1st chaetiger, while remaining dorsal cirri are distinctly fusiform and thick, with yellow granular inclusions. It is also distinguished by details of the chaetae.

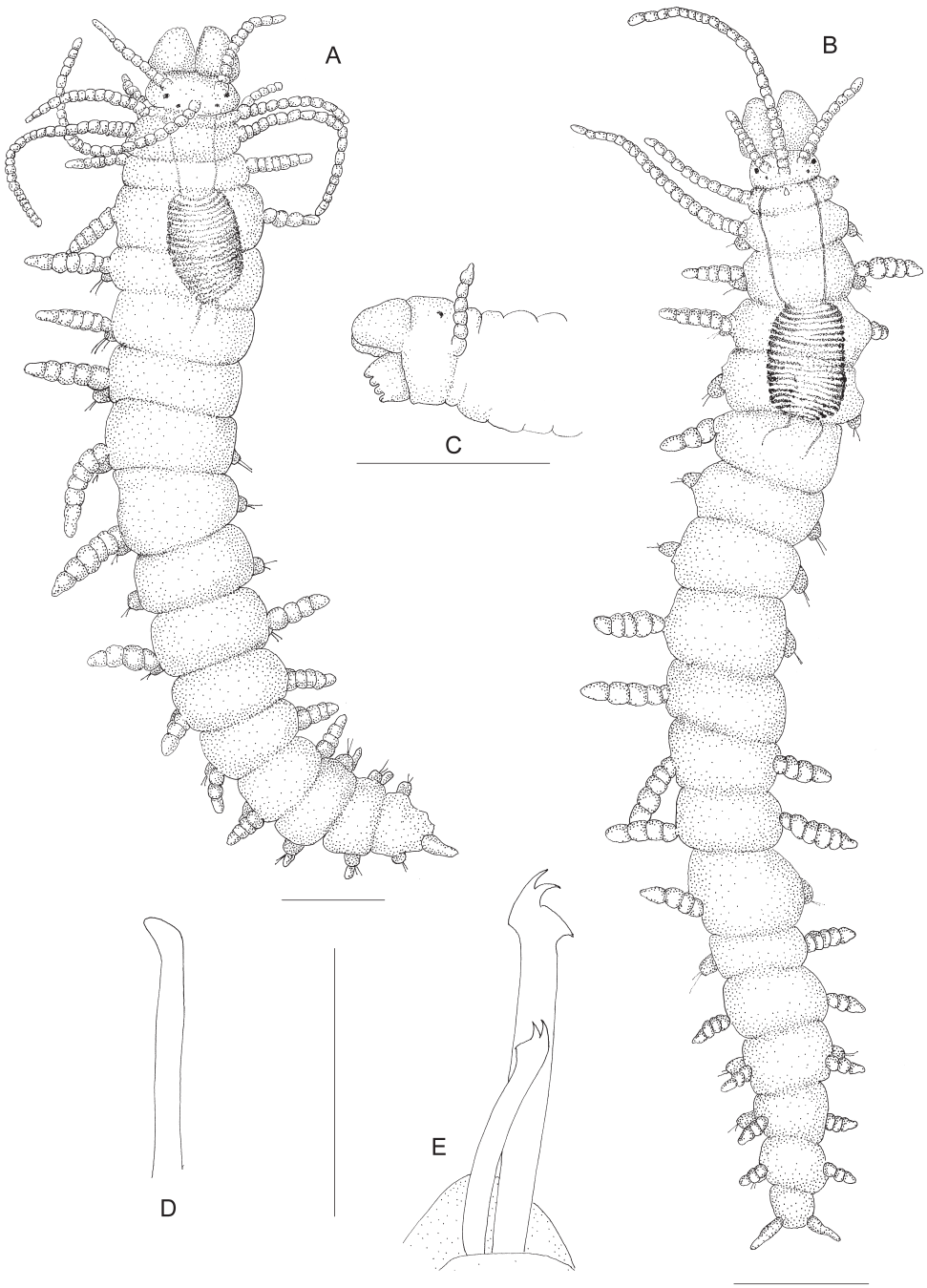

FIG. 1. – *Haplosyllis crassicirrata* n. sp. A: Holotype, dorsal view; B: Paratype1, dorsal view; C: Paratype 2, anterior end, lateral view; D: Acicula, midbody chaetiger; E: Simple chaetae, midbody chaetiger. Scale A-C: 0.3 mm; D: 29 µm; E: 20 µm.

Sardá *et al*. (2002) distinguished two groups of *Haplosyllis* species using relative size, one group with taxa of small size (2-6 mm) and the other with taxa of larger size (more than 6 mm). *Haplosyllis crassicirrata* clearly belongs to the group with small bodies. Probably the most similar species is *Haplosyllis basticola* Sardá, Ávila and Valerie, 2002, living inside the sponge *Ianthella basta* (Pallas, 1776) from Micronesia. However, *H. basticola* has smooth and cylindrical mid-body and posterior dorsal cirri, alternating in length, and has only a single chaeta per parapodium; furthermore, the shape of the chaetae is distinctly different, the teeth at the tip and the main fang are considerably shorter and more rounded (Fig. 2C) than those found in *H. crassicirrata*. *Haplosyllis anthogorgicola* Utinomi,

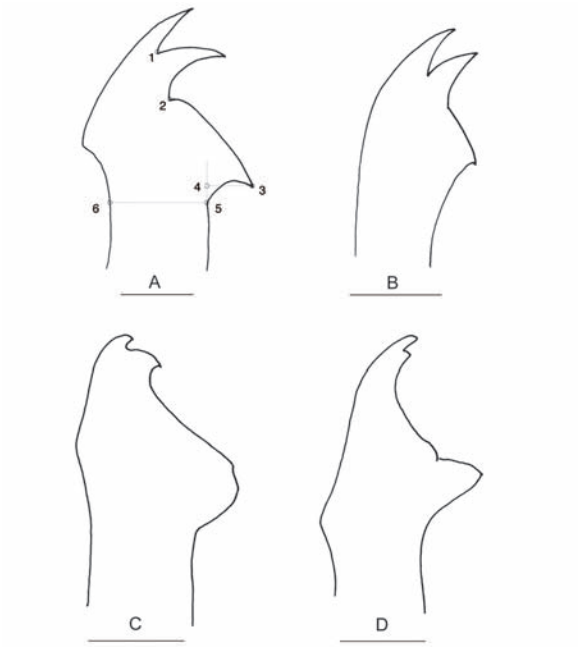

FIG. 2. – A: Large chaeta of *Haplosyllis crassicirrata* n. sp. Measures used to compare the chaetal profile (for largest chaeta after Martín *et al*. 2003); MJ (distance between 1-2), BMF (distance between 2-4), SW (6-5), LMF (distance between 3-4), US (distance between 2-3), LS (distance between 3-5). B: Small chaeta of *Haplosyllis crassicirrata* n. sp. C: Chaeta of *Haplosyllis basticola* (after Sardá *et al*., 2002); D: Chaeta of *Haplosyllis anthogorgicola* (after Utinomi, 1956). Scale A, B: 2 µm; D: 2.5 µm ; E : 12.5 µm.

1956, from Japan, living on the gorgonian *Anthogorgia bocki*, is also similar to the new species, but differs in having cylindrical midbody dorsal cirri, a single chaeta per parapodium, and in the shape of the chaetae, where the teeth at the tip are shorter and the main fang is not curved (Fig. 2D) as in *H. crassicirrata* n. sp. (Utinomi, 1956; Martín *et al*., 2002).

Syllis marugani n. sp.
(Figs. 3, 4)

Material examined: M1. Holotype MNCN 16.01/10143 and Paratypes (3) MNCN 16.01/10144.

Etymology. This species is dedicated to Jesús Marugán for his unconditional support and his always fruitful suggestions to the first author.

Description. Holotype is a mature specimen with stolon (probably male), length for 90 chaetigers 15 mm, width 0.9 mm. Three paratypes, length 11 mm and width 0.8 mm for 63 chaetigers; length 8 mm and width 0.7 mm for 65 chaetigers; and length 7 mm and width 1 mm for 55 chaetigers. Body broad, thick and cylindrical, marked orange-reddish on anterior half, pigment concentrated in small spots on midbody segments becoming lighter to whitish on posterior half of body (ethanol preserved specimens). Prostomium wider than long, partially covered by peristomium, with two pairs of distinct red eyes in a trapezoidal arrangement. Median antenna arising on middle of prostomium, longer than combined length of prostomium and palps, with 16-18 broad articles; lateral antennae similar in shape and length to median one, inserted at anterior margin of prostomium, with 16-18 articles. Palps broad, slightly longer than prostomium. Peristomium similar in length to following segments, with two pairs of tentacular cirri. Dorsal tentacular cirri with 21-22 articles, ventral ones with 11-18 articles (Figs. 3A,B). Dorsal cirri long, broad, slightly longer than body width, anterior ones distinctly broad, all similar in length with about 16-22 articles (Figs. 3A, 4A). On the midbody, some cirri are longer, with 25 articles, and erect and curling over dorsum; and others slightly shorter, with 20 articles, laterally directed (Figs. 3C, 4B). Posterior dorsal cirri longer than those of anterior region with 25-28 articles (Fig. 4C). Ventral cirri short, not extending beyond parapodial lobes, conical on anterior chaetigers and digitiform from midbody (Figs. 4A-C). Anterior parapodia each with 13 compound, heterogomph chaetae, distal part of shafts provided with spines and bidentate blades (31-36 µm length), both teeth similar in size and length, with thin spines on margin (Fig. 4A,D). Midbody chaetigers with 12-13 compound chaetae, shafts with spines, robust and bent, with extended and curved articulation. Blades markedly short (26-28 µm length), with distal tooth longer than proximal one; and about 7-8 thin spines on margin (Fig. 4B,E). Posterior parapodia with about 13 compound chaetae, with spinulate shafts more robust and distally bent than anterior ones; blades similar in length to those of midbody (26-28 µm), provided with two large distal teeth, distal one longer than proximal one, and 3-5 thin, short spines on margin (Figs. 4C,F). Dorsal simple chaetae distally bifid with short subdistal spines on margin (Fig. 3G) and ventral simple chaetae distally bifid, smooth on margin (only seen in last parapodia of one paratype) (Fig. 3F). Three aciculae per parapodium, slightly bent and pointed, more rounded in posterior parapodia (Figs. 4G-I). Pygidium conical, with two long articulated anal cirri, longer than pygidium and last segment together, with 15-17 articles, and one short median papilla (Fig. 3D). Pharynx extending

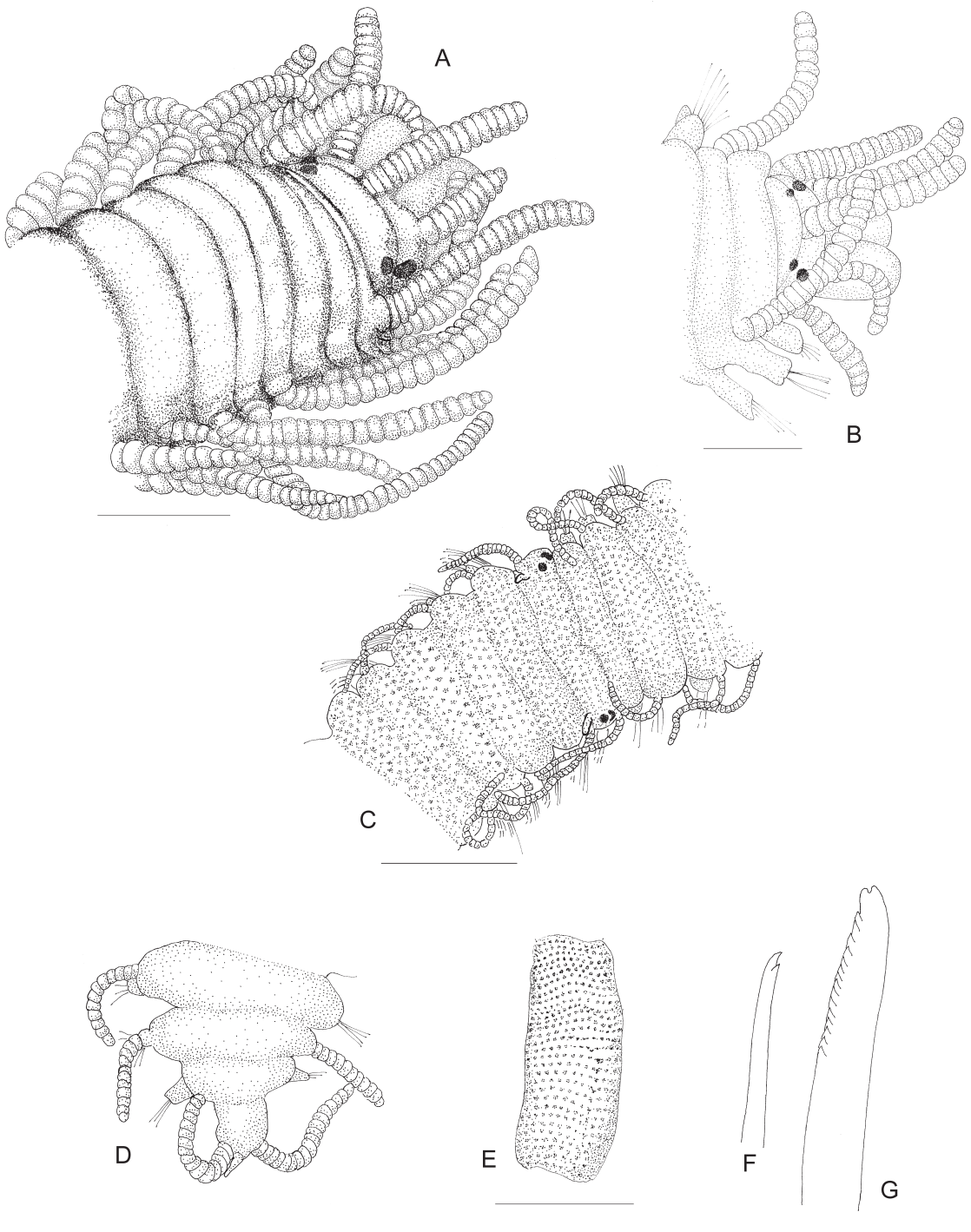

FIG. 3. – *Syllis marugani* n. sp. A: Holotype, anterior end, dorsal view; B: Paratype 1, anterior end, dorsal view; C: Paratype 1, attached stolon, dorsal view, anterior end; D: Paratype 2, posterior end, dorsal view; E: Proventriculus, dorsal view; F: Ventral simple chaeta, posterior chaetiger; G: Dorsal simple chaeta, posterior chaetiger. Scale A, C, E: 0.74 mm; B: 0.38 mm ; D: 0.29 mm.

through 9 segments; conical tooth on anterior margin. Proventricle long, extending through 8 segments, with about 38 cell-rows (Fig. 3E). Holotype and one paratype have developing stolons. Stolon of paratype (70 segments, 1.2 mm length), probably male, *Chaetosyllis* type, starts at chaetiger 52, with two small pairs of red eyes and two small lateral antennae (Fig. 3C).

Remarks. *Syllis marugani* n. sp. is characterized by a markedly orange body pigmentation, thick and long dorsal cirri, and compound chaetae with short

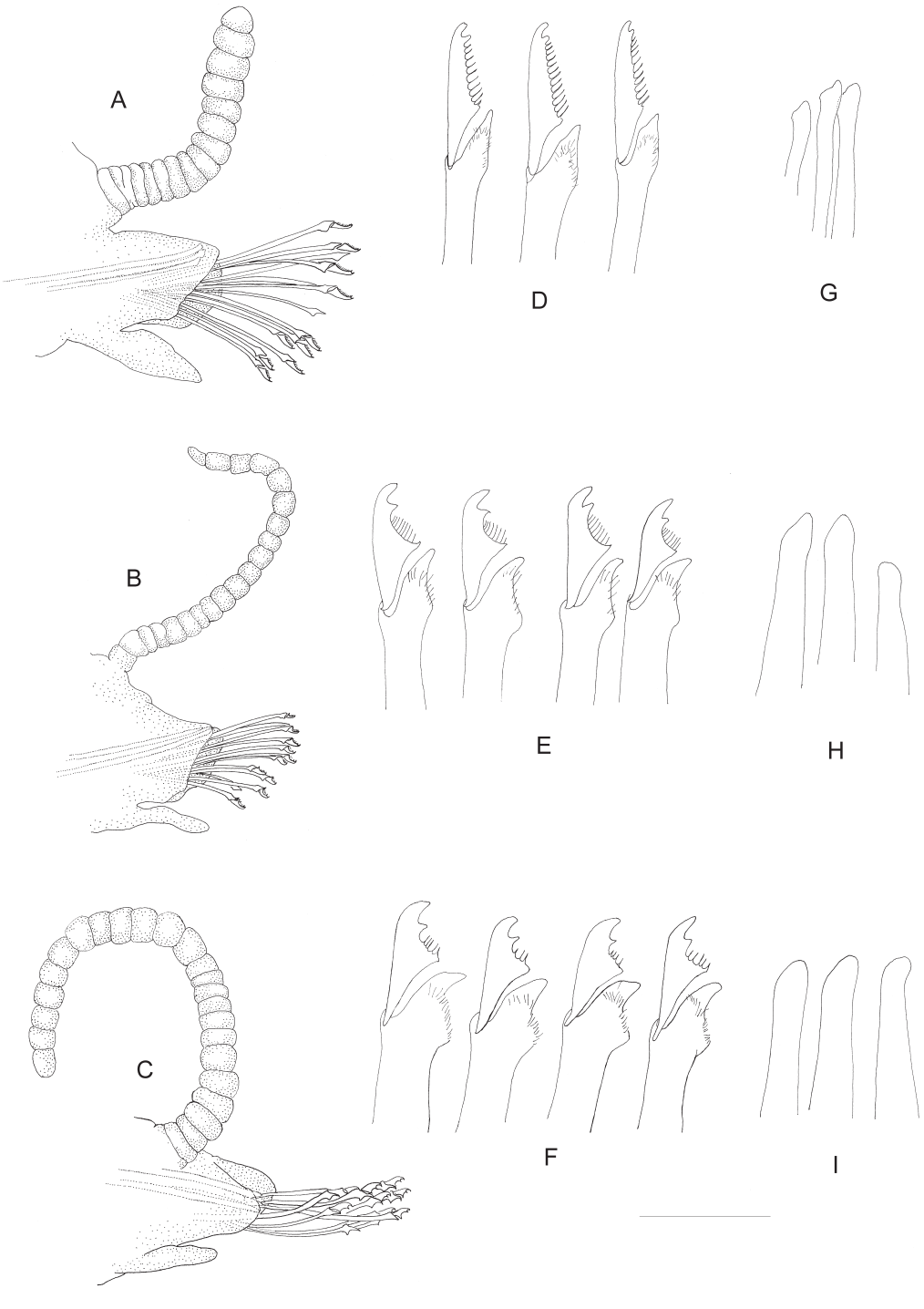

FIG. 4. – *Syllis marugani* n. sp. A: Parapodium, posterior view, anterior chaetiger; B: Parapodium, posterior view, midbody chaetiger; C. Parapodium, posterior view, posterior chaetiger; D: Compound chaetae, anterior chaetiger; E: Compound chaetae, midbody chaetiger; F: Compound chaetae, posterior chaetiger; G: Aciculae, anterior chaetiger; H: Aciculae, midbody chaetiger; I: Aciculae, posterior chaetiger. Scale A, C: 0.18 mm; B: 0.14 mm; D-I: 29 μm

bidentate blades and bent shafts on posterior part of the body. Similar species, however, do not share all of its characteristics (Table 1).

Syllis setoensis Imajima, 1966 and *Syllis krohnii* Ehlers, 1864 share with *S. marugani* the presence of broad dorsal cirri, short blades and bent posterior shafts, but the colour pattern is different, being yellow in *S. setoensis*, reddish with distinct dark red transversal lines in *S. krohnii* and orange in *S. marugani*. Some anterior dorsal cirri in *S. setoensis* and *S.*

TABLE 1. – Principal characteristics of *Syllis marugani* n. sp. and similar species.

	Body pigmentation	Dorsal cirri	Strong alternation in cirri length	Robust and angulated shafts in posterior chaetigers	Blades of compound chaetae in posterior chaetigers	Distribution (Type locality in bold)	References
Syllis marugani n. sp.	Orange	Broad	Absent	Present	Bidentate	Pacific Ocean (**Japan**)	
S yllis setoensis Imajima, 1966	Yellow	Broad	Present	Present	Bidentate	Pacific Ocean (**Japan**)	Imajima, 1966e
Syllis krohnii Ehlers, 1864	Reddish with distinct dark red transversal lines	Broad	Present	Present	Unidentate or slightly bidentate	**Mediterranean Sea**, Red Sea, Atlantic Ocean, Indian Ocean, Pacific Ocean	San Martín, 2003
Syllis monilata Imajima, 1966	Chaetigers 1 and 2 black	Thin	Absent	Present	Bidentate	Pacific Ocean (**Japan**)	Imajima, 1966e
Syllis crassicirrata (Treadwell, 1925)	Very variable with dark dorsal bands	Broad	Present	Absent	Bidentate	Pacific Ocean (**Hawaii Islands**, Polynesian Islands), Indian Ocean (NW Australia)	Hartmann-Schröder, 1965, 1978; Licher, 1999
Syllis nipponica Imajima, 1966	Fith chaetiger dark	Broad	Absent	Absent	Bidentate	Pacific Ocean (**Japan**)	Imajima, 1966e
Syllis okadai Fauvel, 1934	Prostomium, palps, first two and 7th[h]-9th chaetigers dark chocolate coloured	Broad	Absent	Present	Unidentate	Pacific Ocean (**Japan**, Gulf of Siam, Adaman Islands)	Fauvel, 1934; Imajima, 1966e

krohnii are broader than those in *S. marugani* and they have also a more distinct alternation in length and thickness. Compound chaetae in posterior chaetigers of *S. krohnii* are unidentate or slightly bidentate in some cases, while in *S. marugani* they are strongly bidentate.

Syllis monilata Imajima, 1966 has the same kind of posterior chaetae as *S. marugani*, but this species has considerably thinner dorsal cirri, alternating in length. The pigmentation of *S. monilata* is also different with a black dorsum on the first and second chaetigers.

Syllis crassicirrata (Treadwell, 1925) has thick dorsal cirri as has *S. marugani* but it differs in the colour pattern (dark dorsal bands on each segment), alternation in cirri length, shafts of compound chaetae not bent and a distinct posterior acicula, which is markedly thick, acute and protruding out of parapodial lobes.

Syllis nipponica Imajima, 1966 has broad dorsal cirri also, but pigmentation of the body is different (dorsum of 5th chaetiger is dark) and the shafts of the posterior compound chaetae are less sharpened and more curved. *Syllis okadai* Fauvel, 1934 has compound chaetae with thick and curved shafts in posterior chaetigers but the blades are unidentate, and the body pigmentation also differs (prostomium, palps, the first two, and the 7th to 9th chaetigers are dark chocolate coloured).

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Syllidae (Polychaeta) from Japan with the descriptions of three new species

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Abstract

The study of a collection of Japanese Syllidae (Polychaeta) from 18 different intertidal samples has yielded a total of 16 genera and 31 species. Three new species of *Syllis* Lamarck, 1818 from Japan are described. *Syllis multiannulata* n. sp. is mainly characterized by its cylindrical, broad body with annulated segments, weakly articulated antennae and cirri, dorsal cirri originating from two different levels, the presence of pre- and postchaetal parapodial lobes, and the pharynx being shorter than the proventricle. *Syllis pilosa* n. sp. is characterized by the presence of two marked ciliary bands per segment, elongated bidentate compound chaetae, and a very long pharynx and proventricle. *Syllis rubicunda* n. sp. has a broad cylindrical body with distinct colour pattern, long and thick dorsal cirri, bidentate chaetae, and the pharyngeal tooth being slightly removed from the anterior margin. Two species revealing previously unreported characters are also described and illustrated: *Amblyosyllis speciosa* Izuka, 1912 and *Odontosyllis undecimdonta* Imajima and Hartman, 1964. Moreover, one species belonging to the genus *Pionosyllis* Malmgren, 1867 is described, but will remain unnamed until additional material becomes available. An emended diagnosis for *Alcyonosyllis* Glasby and Watson, 2001 and a new combination, *Alcyonosyllis exiliformis* n. comb. are proposed. The generic name *Trypanoseta* Imajima and Hartman, 1964 is proposed to replace *Geminosyllis,* Imajima, 1966 and *Trypanoseta ohma* is described. Additionally, four new

records for Japanese waters have been found: *Eusyllis assimilis* Marenzeller, 1867, *Nudisyllis tinihekea* Knox and Cameron, 1970, *Paraehlersia ehlersiaformis* (Augener, 1913) and *Branchiosyllis exilis* (Gravier, 1900).

Key words new species, *Pionosyllis* sp., Syllidae, Autolytinae, Eusyllinae, Exogoninae, Syllinae, Polychaetes, Taxonomy.

Contents:

Introduction

The wealth of studies on Japanese polychaetes is large. The earliest works are those of Marenzeller (1879), McIntosh (1885), Moore (1903) and Izuka (1912). Subsequent investigations were performed by Fauvel (1934, 1936), Utinomi (1956) and Imajima and Hartman (1964). Thereafter, Imajima (1966a-e) published a series of papers focused on the subfamilies of Syllidae. More recent studies are those of Ohwada (1988) and San Martín and Nishi (2003) describing new species of Syllidae, and those of Imajima (1967, 1994, 1997, 2001, 2003, 2005, 2006) dealing with polychaetes in general, including Syllidae.

In a previous study (Aguado *et al.*, 2006) two new species were described, *Haplosyllis crassicirrata* Aguado, San Martín and Nishi, 2006 and *Syllis marugani* Aguado, San Martín and Nishi, 2006. This study is a contribution from the same authors to extend the knowledge of Syllidae from Japan. In this paper three new species are described: *Syllis multiannulata* n. sp., *Syllis pilosa* n. sp. and *Syllis rubicunda* n. sp. According to the law of priority of the International Code of Zoological Nomenclature, *Trypanoseta* Imajima and Hartman, 1964 is herein proposed to replace *Geminosyllis*, Imajima, 1966. In addition, a broader diagnosis of the genus *Alcyonosyllis* Glasby and Watson, 2001 is provided.

Recently published research on the syllid fauna of Australia (San Martín and Hutchings, 2006; San Martín *et al.*, in press) has been useful in providing a large amount of comparative material. Similarities between the syllid faunas of Australia and Japan have been encountered. Several species previously reported from Japan have been found in Australia (San Martín and Hutchings, 2006; San Martín *et al.*, in press) and, in this study, four species common in Australian waters are reported, which at the same time represent new reports for Japan: *Eusyllis assimilis* Marenzeller, 1867, *Nudisyllis tinihekea* Knox and Cameron, 1970, *Paraehlersia ehlersiaformis* (Augener, 1913) and *Branchiosyllis exilis* (Gravier, 1900). Detailed descriptions, discussion and iconography of these species can be found in San Martín and Hutchings (2006) and San Martín *et al.* (in press). Therefore, only brief descriptions of these Japanese specimens are presented herein. Type series and material loaned by different institutions has also been used for comparison with our material.

Several species examined in this study are considered cosmopolitan since they have

been found in distant geographical areas. Such is the case of *Branchiosyllis exilis* (Gravier, 1900), *Exogone naidina* Örsted, 1845, *Syllis armillaris* (Müller, 1771), *Syllis gracilis* Grube, 1840, *Syllis hyalina* Grube, 1863 and *Trypanosyllis zebra* (Grube, 1860), all relatively frequent species. Several authors have noted that these species could actually be species complexes (Martín and Britayev, 1998; San Martín, 2003; San Martín and Hutchings, 2006), and therefore, a more detailed comparative study of material around the world would be necessary for distinguishing populations or different species currently blurred under the same name. Recently, some authors have made invaluable efforts in establishing valid species and their synonymies in Syllidae, such as Licher (1999) for *Typosyllis* Langerhans, 1879; Nygren (2004) for the Autolytinae; San Martín (2005) for the Exogoninae, San Martín and Hutchings (2006) for the Eusyllinae and San Martín *et al*. (in press) for the Syllinae. Synonymies proposed by these authors have been accepted in this study for the species examined. Subgenera are not accepted herein, following other authors (San Martín, 1992, 2003; Licher, 1999); and in accordance with Böggemann and Westheide (2004) *Exogone* Örsted, 1845 and *Parexogone* Mesnil and Caullery, 1918 are considered as different genera. Finally, *Typosyllis* (*sensu* Licher, 1999) is considered herein as a synonym of *Syllis* Lamarck, 1818, following San Martín (1984, 1992, 2003). Hence, the species *Syllis monilata*, *Syllis pectinans*, and *Syllis nipponica* are new combinations.

Material and methods

A biological survey was carried out along the period 1995-2004 at various Japanese localities mostly on the east coast of Honshu (Shikine Island and Okinawajima Island). A total of 18 samples was collected from the intertidal rocky shore, estuarine muddy bottom, subtidal sea grass beds, shallow sandy bottom and coralline substrata, and rocky shore deep substrata. The specimens were fixed in 10% formaldehyde-seawater and preserved in 70% ethanol solution, except for most of the specimens collected in Manazuru Peninsula, Sagami Bay, which were fixed and preserved in 95% ethanol for molecular studies. For identification, an Olympus SZ30 stereomicroscope and Olympus CH30 optic microscope were used. Drawings were made to scale, with a camera lucida drawing tube in a Nikon Optiphotoptic microscope

equipped with interference contrast optics (Nomarsky). Selected specimens were critical point dried, and then coated with 102 Å of gold for SEM, examined using a Philips XL30 electronic microscope, connected to an EDAX DX4i analyzer at SIDI (Servicio Interdepartamental de Investigación), Universidad Autónoma de Madrid (UAM). Width of specimens was measured at the level of the proventricle, excluding the parapodia. The studied material is deposited at the Kitakyushu Museum of Natural History and Human History, Japan (KMNH), the Coastal Branch of Natural History Museum and Institute, Chiba, Japan (CBM) and the Museo Nacional de Ciencias Naturales, Madrid (MNCN). The comparative material examined has been loaned by the Australian Museum, Sydney (AM), Zoologisch Museum, Universiteit van Amsterdam (ZMA), Muséum Nationale d´Histoire Naturelle, Paris (MNHN) Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt (SMF), Zoologisches Institut und Zoologisches Museum, Universität Hamburg (ZMH), and MNCN.

Systematics

Subfamily Autolytinae Langerhans, 1879

Epigamia noroi (Imajima and Hartman, 1964)

Autolytus noroi Imajima and Hartman, 1964: 97-98, fig. 20A-G. Imajima, 1967: 417.

Autolytus nipponensis Imajima and Hartman, 1964: 96-97, fig. 19A-F.

Autolytus (Regulatus) noroi Imajima, 1966a: 69-71, fig. 22A.

Autolytus (Regulatus) nipponensis Imajima, 1966a: 71-72, fig. 22B-G.

Epigamia noroi Nygren, 2004: 176-177, fig. 89A-E.

Material examined. KMNH IvR 700,135 (1 spec.) Shiraiso Coast, Manazuru, Sagami Bay, 35°09’14’’N 139°08’49’’E, intertidal to subtidal rocky shore, sea grass and algae, coll. by E. Nishi, September 2004.

Distribution. North Pacific Ocean (Japan, California).

***Proceraea vulgaria* (Imajima, 1966)**

Autolytus (Regulatus) vulgarius Imajima, 1966a: 59-61, fig. 17A-J; 1967: 416-417.

Proceraea vulgaria Nygren, 2004: 77-78, fig. 30 A-F.

Material examined. MNCN 16.01/11000 (2 specs) Shiraiso Coast, Manazuru, Sagami Bay, 35°09’14’’N 139°08’49’’E, intertidal to subtidal; rocky shore, sea grass and algae, coll. by E. Nishi; September 2004, fixed and preserved in 95% ethanol.

Remarks. One specimen was dissected to examine the trepan, which has large and small alternating teeth, as described by Imajima (1966a) and Nygren (2004). The other specimen has a developing stolon.

Distribution. North West Pacific Ocean (Japan).

Subfamily Eusyllinae Malaquin, 1893

***Amblyosyllis speciosa* Izuka, 1912**

Figs 1, 2

Amblyosyllis speciosa Izuka, 1912: 183-184. Imajima and Hartman, 1964: 106-108, pl. 3, Figs a-i. Imajima, 1966b: 86-88, fig. 27; 1967: 417; 2003: 141-142; 2006: 352. Dorsey, 1978: 22-24, fig. 1a-c.

Amblyosyllis nigrolineata Okada, 1934: 317-320, Figs 1, 2.

Material examined. KMNH IvR 700,136 (1 spec). Ubara, Katsuura, Boso Peninsula, 35°07’52’’N 140°16’55’’E, intertidal rocky shore, coll. by T. Noichi, June 1995. KMNH IvR 700,137, IvR 700,201 (2 specs), MNCN 16.01/11004 (1 spec.) Ubara, Katsuura, Boso Peninsula, 35°07’55’’N 140°17’16’’E, intertidal rocky shore, sea grass and algae, coll. by E. Nishi, September 1995. KMNH IvR 700,138 (1 spec.) Ubara, Katsuura, Boso Peninsula, 35°07’52’’N 140°16’55’’E, intertidal rocky shore, coll. by T. Noichi, October 1995.

Description

All specimens incomplete, epigamic; best preserved specimen KMNH IvR 700,137 a mature female, anterior fragment 2.5 mm long, 0.6 mm wide, with six chaetigers. Body fragile,

pigmented with one posterior transverse dark band on each segment, with median rhomboidal mark (Fig. 1A). Segments typically trapezoidal in shape, especially those of midbody, intersegmental constrictions strongly marked (Figs 1A; 2A). Segments with wrinkles arranged in several bands, more or less transversal, more visible on posterior part of each segment (Figs 1G; 2B). Prostomium oval, posteriorly notched, with four large red eyes in trapezoidal arrangement (Fig. 1A), anterior pair visible in ventral view. Antennae long, inserted on anterior margin of prostomium, with distinct ceratophores, median one more than twice as long (about 45 articles) as lateral ones (30 articles) (Fig. 1A). Palps basally fused, divergent, ventrally folded, (Fig. 1F) difficult to see dorsally (Fig. 1A). Peristomium shorter than subsequent segments, with two pairs of tentacular cirri, missing in all specimens except in KMNH IvR 700,137 (15 articles). Two elongate nuchal lappets with long and numerous cilia on margins (Fig. 1A), extending to chaetiger 2. Most of dorsal cirri detached, when present long, distinctly annulated except at bases (20-40 articles) with yellow to orange granular material inside, distributed in two longitudinal rows (Fig. 1B) and some small papillae over the surface (Fig. 2C). Parapodial lobes long, conical, with long, digitiform prechaetal lobe, distally pointed (Figs 1B; 2A). Ventral cirri spindle shaped, large, broad, arising ventro-laterally, inserted on middle of parapodia, with dark granular material inside, distributed in two rows (Fig. 1B) and some small surface papillae (Fig. 2D). Parapodia with about 20 compound, heterogomph chaetae (Fig. 1B), blades distinctly bidentate (Figs 1D, E; 2E-H); blades decreasing in length (Fig. 1D) within fascicle from dorsal (77 µm) to ventral (50 µm), with short spines on margin. Specimens KMNH IvR 700, 136 and KMNH IvR 700,138 with shorter blades (64 µm dorsally, 42 µm ventrally) (Fig. 1E). Three straight and pointed aciculae per parapodia (Fig. 1C). Modified segments from fifth chaetiger with three notoaciculae protruding from parapodia and about 20 capillary notochaetae, modification from sixth segment posteriorly in specimen KMNH IvR 700,136. Triangular pygidium and two wide and long anal cirri, similar in length to dorsal ones. Pharynx slender, with several coils, three in specimen KMNH IvR 700,137 (Fig. 1A), one to two in specimen KMNH IvR 700,136. Trepan composed by six pentacuspid teeth (Fig. 1H). Proventricle extending through 1.5 segments, with 11-13 muscle cell rows (Fig. 1A).

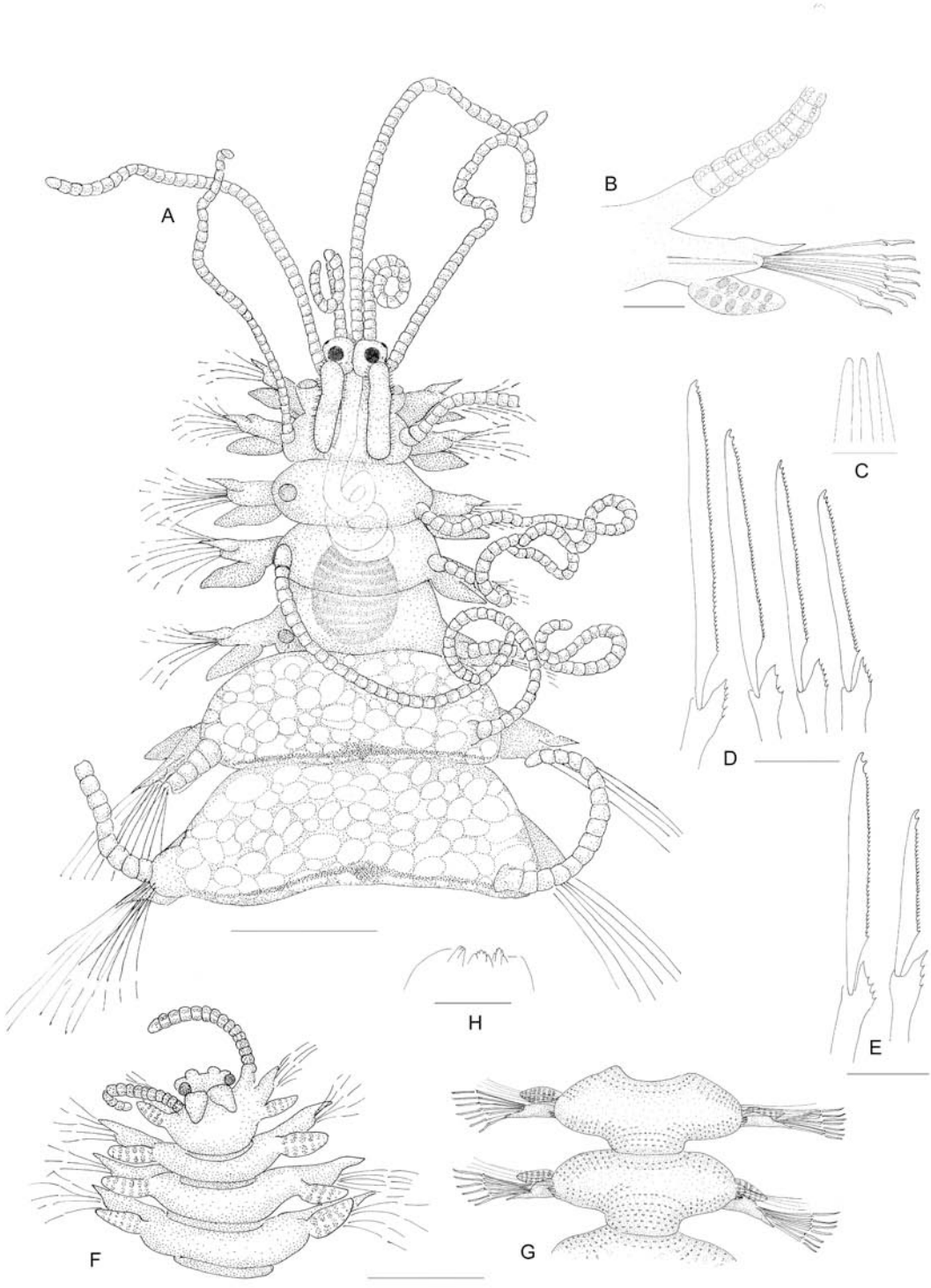

Figure 1. *Amblyosyllis speciosa*: A, Anterior end, dorsal view KMNH IvR 700,137; B, Midbody parapodia, anterior view KMNH IvR 700,137; C, Mibody aciculae, KMNH IvR 700,137; D, Midbody chaetae KMNH IvR 700,137; E, Midbody chaetae, KMNH IvR 700,136; F, Anterior end, ventral view KMNH IvR 700,201; G, Midbody segments, dorsal view KMNH IvR 700,137; H, Trepan KMNH IvR 700,137. Scale A: 0.5 mm; B: 0.2 mm; C-E: 20 µm; F, G: 0.4 mm; H: 48 µm.

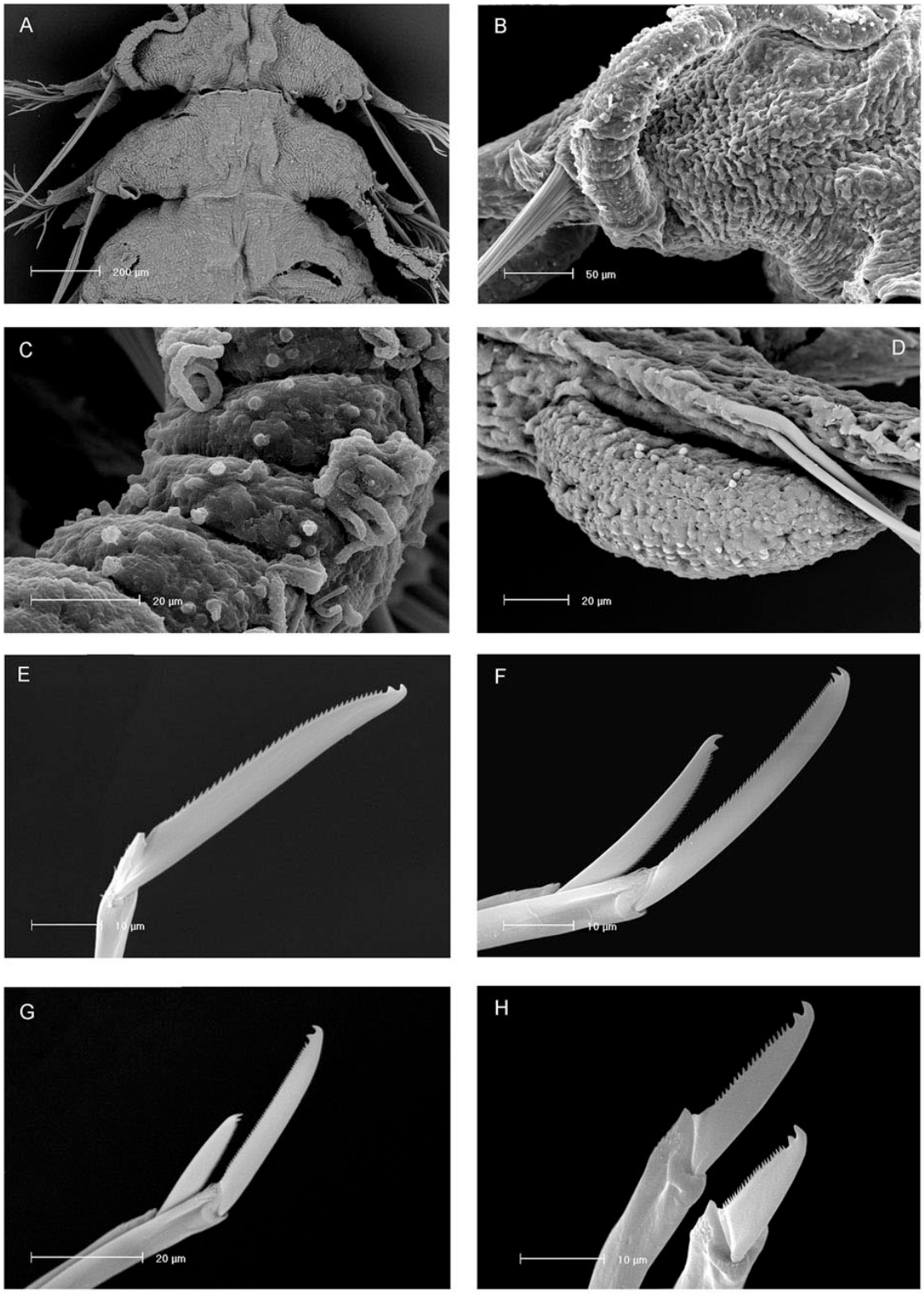

Figure 2. *Amblyosyllis speciosa*. SEM. MNCN 16.01/11004: A, Midbody segments, dorsal view; B, Dorsal surface of midbody segment; C, Papillae on dorsal cirri, midbody segment; D, Ventral cirri, midbody segment; E, Most dorsal midbody chaeta; F-G, Midbody chaetae, medially located in the chaetal fascicle; H, Most ventral midbody chaetae.

Remarks

All the specimens examined in this study show the same colour pattern, i. e. in dark transversal lines per segment with a triangular spot in the middle, described by Imajima and Hartman (1964) and Imajima (1966b). We found some variation in the length of the blades, being slightly shorter in specimens KMNH IvR 700,136 and 138 (more similar to previous descriptions) than they are in specimen KMNH IvR 700,137. However, all the specimens agreed otherwise with the earlier descriptions. The teeth of the trepan are pentacuspid in all the cases, differentiating them from the species *Amblyosyllis lineata* Grube, 1864, which has a similar colour pattern, but teeth are tricuspid (Imajima, 1966b; Dorsey, 1978). The organized bands of wrinkles on the surface of the body, and papillae on the dorsal and ventral cirri, are characters that have not been previously reported for this species or any other of the genus. Epigamic modifications have been described for several species of the genus, including *A. speciosa* (Dorsey, 1978; Pettibone, 1963; San Martín and Hutchings, 2006), which is also known to brood eggs in a gelatinous mass (Pernet, 1998).

Distribution. North Pacific Ocean (California, Japan).

Eusyllis assimilis Marenzeller, 1875

Eusyllis assimilis Marenzeller, 1875: 158. San Martín, 2003: 114-117, Figs 52, 53. San Martín and Hutchings, 2006: 273-276, figs 10A-J, 11A-F, 12A-C.

Material examined. KMNH IvR 700,139 (1 spec.) Ubara, Katsuura, Boso Peninsula, 35°07’55’’N 140°17’16’’E, intertidal rocky shore, sea grass and algae, coll. by E. Nishi, April 1998.

Comparative material examined. AM W28942 (1 spec.) Australia, New South Wales, SW side of South Solitary Is. 30°12'S 153°16'E, coral rubble, 18 m, 24 Jun 1992. AM W28941 (5 specs) Western Australia, Red Bluff, Kalbarri, 27° 42'S 114° 09'E, mixed coralline algae on rocky shore, 3.5 m, 10 Jan. 1984; identified by San Martín and Hutchings (2006). ZMA V.Pol. 5254. (1 spec.) Indonesia, NE coast of Sumba, 09°57'S 120°48'E, sandy bottom with sponges and gorgonians, 50 m, Snellius II Expedition, 16.09.1984; identified by Aguado, San Martín and Ten Hove (in press).

Description

Prostomium oval, four eyes in open trapezoidal arrangement; antennae long, slender, irregularly pseudoarticulated; lateral antennae inserted near anterior margin of prostomium, median antenna arising slightly posteriorly to lateral ones. Palps broad, similar in length to prostomium. Peristomium shorter than subsequent segments; dorsal tentacular cirri long, longer than median antenna, ventral tentacular cirri shorter than dorsal ones. Occipital flap present. Dorsal cirri of chaetiger 1 elongated, subsequent dorsal cirri irregularly alternating long cirri, slightly longer than half of body width, and others distinctly shorter, all smooth. Parapodia with prechaetal lobes. Ventral cirri triangular, shorter than parapodial lobes. Some compound chaetae slender, blades bidentate, both teeth similar, and short spines on margin; others, more ventrally located in chaetal fascicle, with shorter and larger blades, strongly bidentate, proximal tooth becoming longer and stouter towards posterior parapodia. Dorsal simple chaetae only on posterior parapodia, unidentate, with small spines on margin. Ventral simple chaetae not seen. Two aciculae on anterior parapodia, with slightly bent tip; only one on posterior parapodia, thicker than anterior ones. Pharynx through eight to nine segments, with a distal crown of papillae; pharyngeal tooth large, located on anterior margin; trepan incomplete. Proventricle elongate, similar in length to pharynx.

Remarks

San Martín and Hutchings (2006) compared material from the Mediterranean Sea with their material from Australia concluding that there was no distinguishable morphological feature to define the Australian population as a different species, although the geographic distribution of this species is disjunct. The studied specimen from Japan broadly coincides with the Australian material and, is therefore identified as *E. assimilis*. Subsequently, the same species has been found among material from Indonesia (Aguado *et al.*, in press). A molecular study would be useful to find out if this is a widely distributed species or a suite of sibling species.

Distribution. East Atlantic Ocean (from English channel to South Africa), Mediterranean Sea, West Pacific Ocean (Japan, New Zealand, Australia), Indian Ocean (Australia, Indonesia).

Eusyllis lamelligera Marion and Bobretzky, 1875

Eusyllis lamelligera Marion and Bobretzky, 1875: 33. San Martín, 2003: 117-120, figs 54, 55. San Martín and Hutchings, 2006: 278-270, figs 15A-J, 16A-F.

Eusyllis habei Imajima, 1966b: 96-98, fig. 31; 1967: 418.

Material examined. KMNH IvR 700,140 (1 spec.) Ubara, Katsuura, Boso Peninsula, 35°07'52''N 140°16'55''E, intertidal rocky shore, coll. by T. Noichi, June 1995.

Comparative material examined. AM W28960 (1 spec.) Australia, New South Wales, N side of Bannister Head, N of Ulladulla, 35°19.15'S 150°29.12'E, grey sponge from top of boulder, 18 m, 6 May 1997. AM W28961 (5 specs) Western Australia, N end of Long Is. 28°27.9'S 113°46.3'E, dead coral substratum covered in coralline and brown algae, 5.5 m, 22 May 1994; identified by San Martín and Hutchings (2006). ZMA V.Pol. 5255. (1 spec.) Indonesia, NE coast of Sumba, 09°57'S 120°49'E, 45 m, sandy bottom and sponges, Snellius II Expedition, 16 September 1984; identified by Aguado, San Martín and Ten Hove (in press).

Remarks

The specimens agree with material from Australia and Indonesia. Imajima (1966b) described the species *E. habei* as differing from *E. lamelligera* by the different pharyngeal denticulation, being incomplete in *E. habei* and complete in *E. lamelligera*, as described by Fauvel (1923). However, the distribution of denticles in *E. lamelligera* is rather variable. From personal observations we know that small specimens may have minute, almost indistinguishable denticles, and others may have distinct ones; we also found some specimens with a higher number of denticles than others. In the Mediterranean specimens, the dorsal part of the pharyngeal margin lacks denticles, whereas in the ventral part they form a more or less developed ventral arc (San Martín, 2003). For these reasons, *E. habei* is considered to be synonymous with *E. lamelligera*.

Distribution. West Atlantic Ocean (North coast of U.S.A. to Cuba), East Atlantic Ocean (from The Channel to Canary Islands), Mediterranean Sea, West Pacific Ocean (Australia, Japan), Indian Ocean (Australia, Indonesia).

Nudisyllis tinihekea Knox and Cameron, 1970

Nudisyllis tinihekea Knox and Cameron, 1970: 77, figs 6-9. San Martín and Hutchings, 2006: 281, fig. 17A-F.

Pionosyllis pulligera Non Krohn, 1852: 251. Augener, 1913a: 221, pl. II, fig. 8, text-fig. 29.

Pionosyllis samsonensis Hartmann-Schröder, 1980: 52, figs 39-43; 1981: 32; 1982: 65. 1983: 130; 1984: 20; 1985: 69; 1986: 41; 1987: 38; 1991a: 35.

Material examined. KMNH IvR 700,141 (1 spec.) Ubara, Katsuura, Boso Peninsula, 35°07’55’’N 140°17’16’’E, intertidal coarse sand, sea grass and algae, coll. by E. Nishi, April 1995.

Comparative material examined. AM W28966 (1 spec.) Australia, New South Wales, Barrenjoey Head, Broken Bay, 33°35'S 151°20'E, algae on rocky substratum, 4 m, 22 Apr. 1983. AM W28970 (5 specs) Western Australia, Red Bluff, Kalbarri, 27°42'S 114°09'E, mixed coralline algae on rocky shore, 3.5 m, 10 Jan. 1984; identified by San Martín and Hutchings (2006).

Description

Body fragile. Prostomium with four eyes in trapezoidal arrangement; median antenna inserted on middle, fusiform; lateral antennae inserted on anterior margin, slightly shorter than median one. Palps broad, oval. Peristomium dorsally reduced; dorsal tentacular cirri long, about twice as long as median antenna; ventral tentacular cirri shorter. Dorsal cirri smooth, thick, long on anterior segments, alternating in length after proventricle. Ventral cirri digitiform, shorter than parapodial lobes. Compound chaetae similar throughout, blades elongated, unidentate, longer ones with subdistal spine, smooth or with fine spines on margin; dorso-ventral gradation in length within fascicle. Dorsal and ventral simple chaetae on posterior parapodia, slender, smooth, unidentate. Acicula solitary, distally tricuspidate. Pharynx short, through two segments; single pharyngeal tooth near anterior margin. Proventricle barrel-shaped, similar in length to pharynx.

Remarks

This is a species widely distributed in Australia (San Martín and Hutchings, 2006) and also previously reported in other areas of the West Pacific Ocean. The Japanese specimen agreed in all characters with Australian material.

Distribution. West Pacific Ocean (New Zealand, Australia, Japan), Indian Ocean (Australia).

Odontosyllis fulgurans (Audouin and Milne Edwards, 1833)

Syllis fulgurans Audouin and Milne Edwards, 1833: 229

Odontosyllis fulgurans japonica Imajima, 1966b: 109-111, fig. 35; 1997: 174; 2001 :59.

Odonthosyllis fulgurans San Martín, 2003: 104-106, fig.46.

Material examined. KMNH IvR 700,142, 700,143 (2 specs) Ubara, Katsuura, Boso Peninsula, 35°07'55''N 140°17'16''E, intertidal rocky shore, sea grass and algae, coll. by E. Nishi, September 1995. KMNH IvR 700,144 (1 spec.) Amaha harbour, Uchibo, Tokyo Bay, 35º 31'N 139º 49'E, 100-200 m, rocky shore, coll. by E. Nishi, October 1996. KMNH IvR 700,145-700,154 (10 specs and 7 stolons) Ubara, Katsuura, Boso Peninsula, 35°07'52''N 140°16'55''E, intertidal rocky shore, coll. by T. Noichi, October 1995.

Comparative Material examined. *Odontosyllis fulgurans*: MNCN 16.01/7570-7580 (numerous specs) Mediterranean Sea, Iberian Peninsula; identified by San Martín (2003).

Remarks

Imajima (1966b) erected a new subspecies, *O. fulgurans japonica*, because the Japanese specimens presented some differences in comparison with material from the Mediterranean Sea. These differences were: the insertion of median antenna (anterior on *O. fulgurans japonica* and supposedly posterior in *O. fulgurans*), occipital flap oval in shape instead of circular, presence of ventral simple chaeta on posterior segments, and the presence of dorsal ciliary bands. However, detailed studies with SEM of Mediterranean specimens of *O. fulgurans* (San Martín, 2003) revealed that the median antenna is inserted on the same position as on Japanese specimens, some specimens had ventral simple chaetae and dorsal ciliary bands. The shape of the occipital flap is not considered here to be a valid difference as it can be slightly modified by the contraction of the prostomium. Therefore, the Japanese specimens closely resemble specimens from Mediterranean and European Atlantic coast, and are considered to belong to the same species.

Distribution. Apparently cosmopolitan.

Odontosyllis undecimdonta Imajima and Hartman, 1964

Figs 3,4

Odontosyllis undecimdonta Imajima and Hartman, 1964: 114-116, pl. 26, figs h-I, pl. 27, figs a-e. Imajima, 1966b: 111; 2003: 145; 2006: 353.

Material examined. KMNH IvR 700,155-700,157 (3 specs), MNCN 16.01/11005 (1 spec.) Ubara, Katsuura, Boso Peninsula, 35°07'55''N 140°17'16''E, intertidal rocky shore, sea grass and algae, coll. by E. Nishi, September 1995. KMNH IvR 700,158 (1 spec.) Ubara, Katsuura, Boso Peninsula 35°07'52''N 140°16'55''E, intertidal rocky shore, coll. by T. Noichi, October 1995.

Description

Longest specimen 13 mm long, incomplete, 1.3 mm wide, with 71 segments, epigamic. Dorsum distinctly arched, ventrally flattened. Specimens with marked dorsal coloration pattern consisting in a single rectangular to rhomboidal mark, strongly red pigmented, medially on each segment, and a dark lateral area, as well as one or two dark transverse bands on dorsum of some segments (Fig. 3A). One transversal ciliary band per segment, dorsally and ventrally (Figs 4A, C, D). Prostomium wider than long, rectangular to oval, with two pairs of large, red eyes, anterior ones slightly larger; eye spots absent (Figs 3A; 4A). Palps broad, fused at bases, similar in length to prostomium, ventrally folded (Fig. 4C). Antennae, tentacular cirri and dorsal cirri pseudoarticulated. Median antenna longer than combined length of prostomium and palps, inserted medially on prostomium (Figs 3A; 4A). Lateral antennae inserted near base of median antenna. Transversal ciliary band across prostomium between pairs of eyes to base of median antenna (Fig. 4B). A pair of ciliary nuchal ridges extending along posterior margin of prostomium, visible laterally (Fig. 4B). Peristomium shorter than following segments. Occipital flap arising from peristomium and partially covering posterior end of prostomium, darkly pigmented, with anterior margin densely ciliated (Figs 3A; 4A, B). Dorsal tentacular cirri long, about double length of median antenna, ventral pair shorter. Dorsal cirri alternating in length, longer ones approximately twice as long as shorter ones, similar in length to body width (Fig. 3A). Cirrophores present on all segments. Ventral cirri conical, broad at base, proximally inserted, not extending beyond tips of parapodia (Fig. 3B). Pre- and postchaetal lobes present on all parapodia, both similar in length (Figs 4E, F).

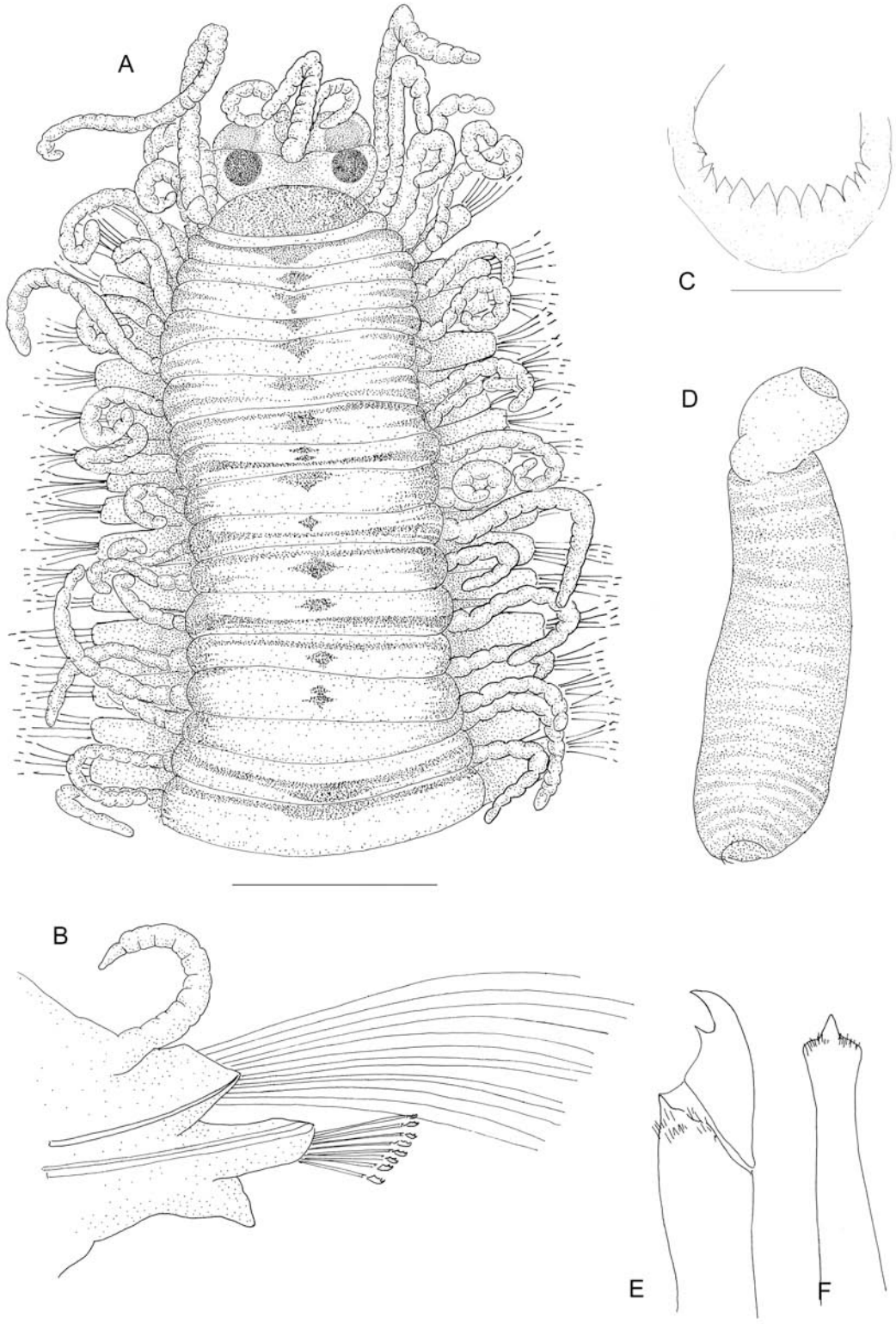

Figure 3. *Odonthosyllis undecimdonta*. KMNH IvR 700,155: A, Anterior end, dorsal view; B, Posterior parapodia, anterior view; C, Trepan; D, Pharynx and proventricle; E, Midbody chaeta; F, Midbody acicula. Scale A, D, 1 mm; B, 0.4 mm; C, 0.2 mm; E, F, 20 µm.

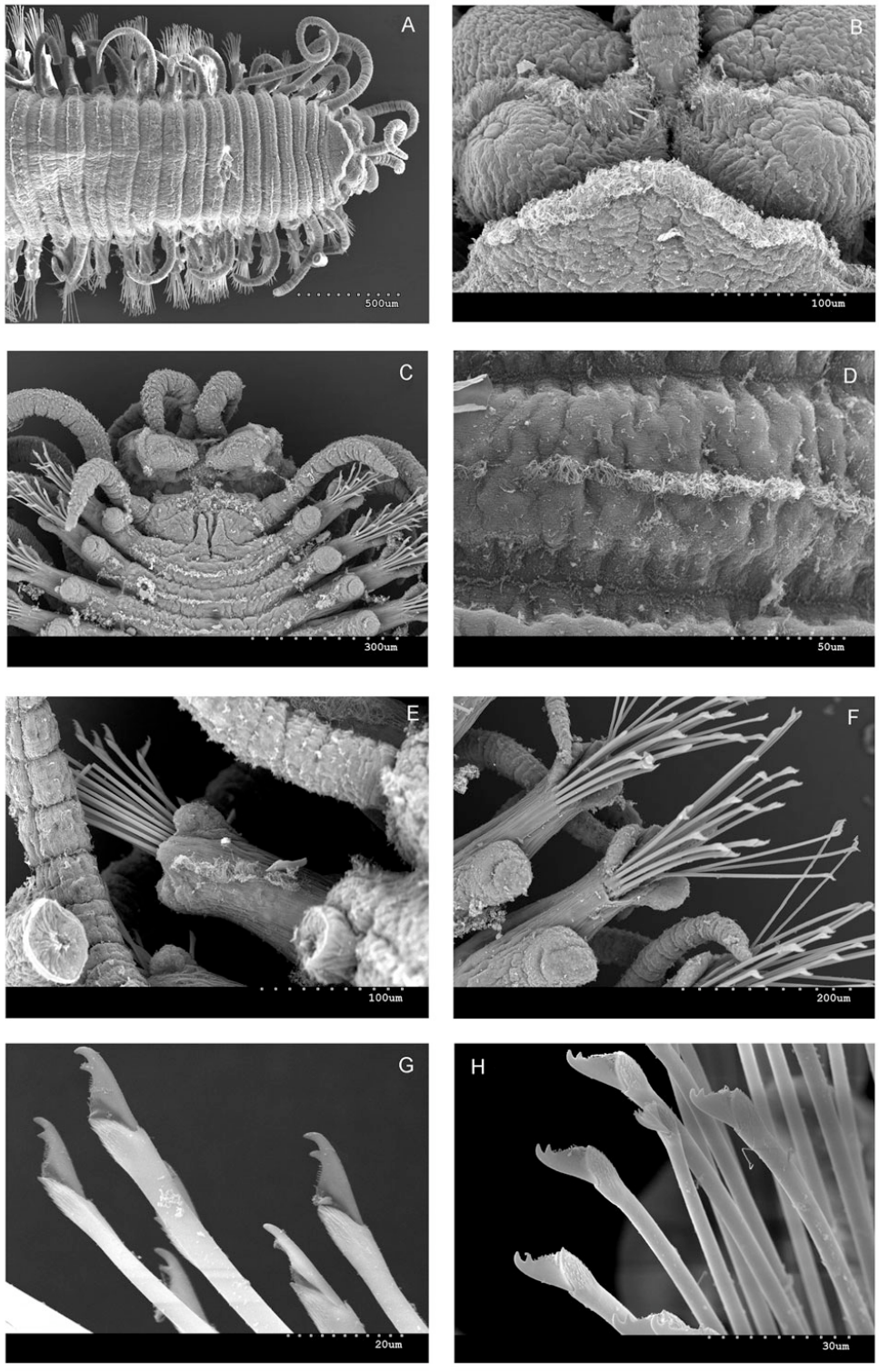

Figure 4. *Odontosyllis undecimdonta*. SEM. MNCN 16.01/11005. A, Anterior end, dorsal view; B, Prostomium and peristomium, dorsal view; C, Anterior end, ventral view; D, Midbody segment, dorsal view; E, Midbody parapodia, dorsal view; F, Midbody parapodia, ventral view; G, Midbody chaetae; H, Posterior chaetae.

Chaetal fascicle with about 20 heterogomph compound chaetae. Short bidentate blades with curved distal tooth, longer and larger than proximal one and short spines on edge, distal part of shafts also provided with small spines (Figs 3E; 4G, H). Inverse gradation in length, with most dorsal blade smallest and most ventral one, longest (8 µm, and 38 µm, respectively on median parapodia) (Fig. 3B). Dorsal and ventral simple chaetae not seen. Three tricuspid aciculae in anterior parapodia with small distal spines (Fig. 3F). Pygidium lacking on all specimens. Some specimens with pygidium regenerating. Pharynx shorter than proventricle (Fig. 3D), with 10 distal papillae on anterior margin and trepan with 11 triangular teeth, decreasing in size laterally (Fig. 3C). Proventricle long, rectangular, not visible, with about 80 cell-rows after dissection (Fig. 5D). Notochaetae and notoaciculae appearing from chaetiger 27 (Fig. 5B).

Remarks

The presence of cilia on the anterior margin of the occipital flap, ciliary bands on the prostomium, number of cell rows in the proventricle, presence of one ciliary band on anterior segments and reproduction by epigamy have not previously been described (Imajima and Hartman, 1964; Imajima, 1966b, 2003).

Distribution. North West Pacific Ocean (Japan).

Paraehlersia ehlersiaeformis (Augener, 1913)

Pionosyllis ehlersiaeformis Augener, 1913a: 225, figs 31, 32.

Syllis (Ehlersia) ferrugina Non Langerhans, 1881: 104. Haswell, 1920a: 101, pl. 12, figs 3-10.

Typosyllis (Langerhansia) ferrugina Non Langerhans, 1881: 104. Hartmann-Schröder, 1981: 30; 1987: 37; 1989: 23; 1991a: 33.

Paraehlersia ehlersiaeformis San Martín and Hutchings, 2006: 309-312, figs 43D-F, 44A-K, 45A-F, 46A-C.

Material examined. KMNH IvR 700,159, 700,160 (2 specs) Nakagusuku Bay, Okinawajima-Island, Ryukyu Archipelago, 26º05'N 127º42'E, intertidal rocky shore with sponges, coll. by K. Tanaka, November 2003.

Comparative material examined. AM W28939 (22 specs) Australia, New South Wales, Taupo Seamount, Tasman Sea, 33°16.85'S 156°09.15'E, limestone and sand bottom, 244 m, 2

May 1989. AM W28377 (4 specs) Western Australia, NE entrance to Goss Passage, Beacon Is., 28° 27.9'S 113°46.7'E, dead branching of *Acropora*, coralline & brown algae, 24 m, 25 May 1994; identified by San Martín and Hutchings (2006).

Description

Body without colour markings. Prostomium oval to circular, four eyes in trapezoidal arrangement. Median antenna long, slender, inserted on middle of prostomium; lateral ones inserted on anterior margin of prostomium. Palps triangular, slightly longer than prostomium. Peristomium similar in length to subsequent segments; tentacular cirri similar to antennae, dorsal ones longer than lateral antennae, ventral ones shorter. Anterior dorsal cirri irregularly articulated becoming smooth and shorter than anterior ones towards posterior segments. Dorsum of each segment with rows of cilia. Subcirral papilla small, present on anterior and midbody segments. Ventral cirri digitiform, similar in length to parapodial lobes. Compound chaetae most dorsally located on the fascicle with elongated, slender blades, bidentate with both teeth similar and short spines on margin; remaining chaetae with shorter blades, bidentate, both teeth similar. Dorsal simple chaetae on posterior parapodia, distally bifid, with short subdistal spines. Ventral simple chaetae on posterior segments, smooth, bidentate, proximal tooth larger than distal one. Anterior parapodia with three aciculae, only one on posterior parapodia, all distally acuminate or lancet-shaped. Pharynx through seven segments; pharyngeal tooth on anterior margin. Proventricle shorter than pharynx.

Remarks

This species has been widely reported in all kind of substrata in all states of Australia (Pacific and Indian Ocean) (San Martín and Hutchigs, 2006). The Japanese specimens perfectly agree with the comparative material.

Distribution. Indian Ocean (Australia). West Pacific Ocean (Australia, Japan).

***Pionosyllis* sp.**

Fig. 5

Material examined. MNCN 16.01/10140 (1 spec.) Ubara, Katsuura, Boso Peninsula, 35°07’55’’N 140°17’16’’E, intertidal rocky shore, sea grass and algae, coll. by E. Nishi, September 1995.

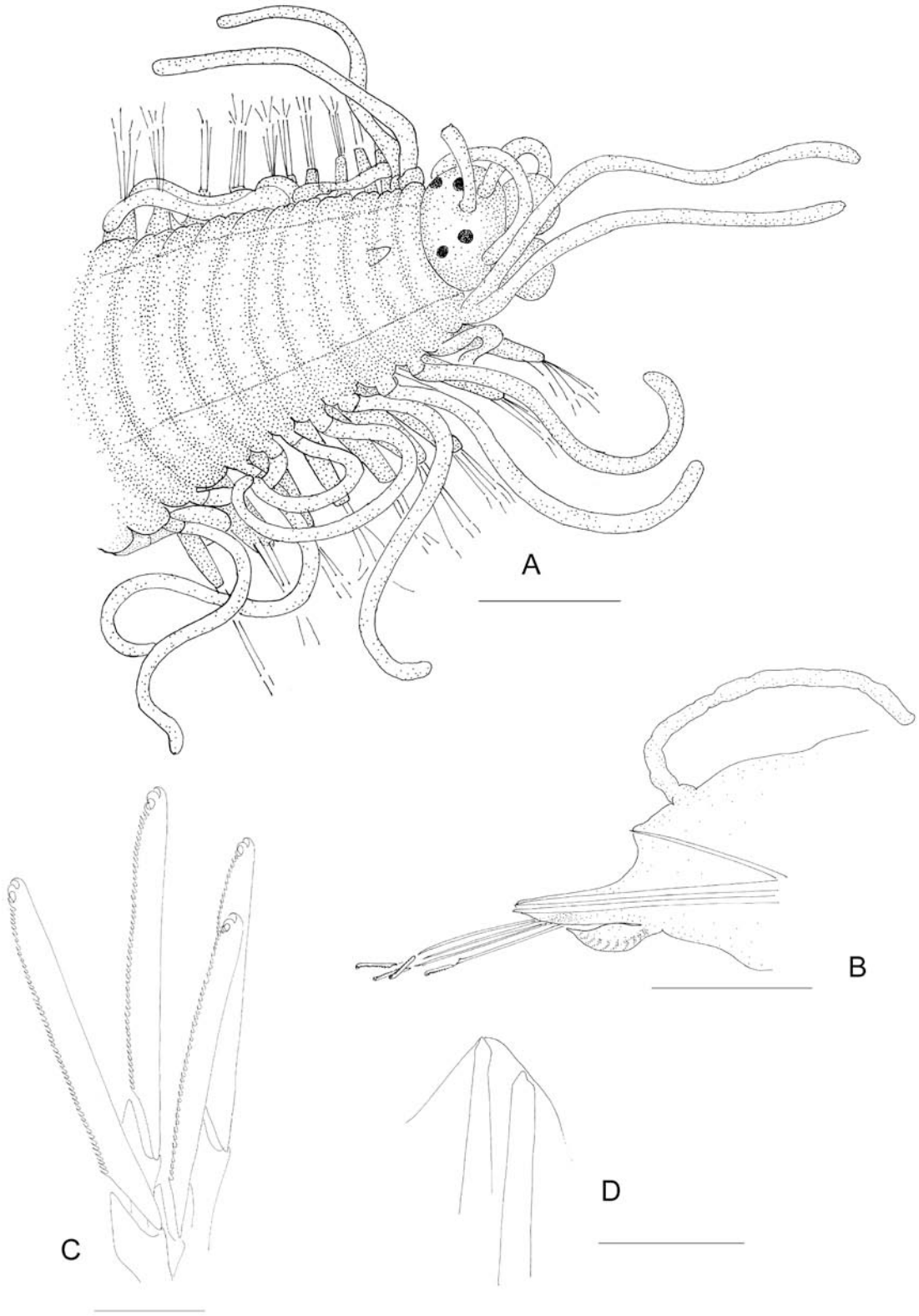

Figure 5. *Pionosyllis* sp. MNCN 16.01/10140: A, Anterior end, dorsal view; B, Parapodium, anterior view, anterior chaetiger; C, Anterior chaetae; D, Anterior aciculae. Scale A, B: 0.4 mm; C, D: 20 µm.

Description

Epigamic specimen, anterior fragment 4 mm long, 0.9 mm wide for 41 chaetigers. Body broad, dorsally arched, light orange coloured. Prostomium oval, with four bright red eyes in open trapezoidal arrangement. Median antenna broken, arising from middle of prostomium; lateral antennae inserted near anterior margin of prostomium, long. Palps cylindrical, completely separated, close at bases (Fig. 5A). Peristomium with long tentacular cirri, slightly shorter than lateral antennae. Ventral tentacular cirri shorter than dorsal ones (Fig. 5A). Anteriormost segments short, becoming longer from proventricular onwards. Dorsal cirri smooth, with distinct elongated cirrophore. Ventral cirri short, not extending beyond parapodial lobes, conical (Fig. 5B). Parapodia with nine to 13 compound heterogomph chaetae, elongated (69-59 µm length), with short spines on margin, distinctly bidentate, distal tooth hooked, and proximal tooth larger and curved, with tendon contacting with margin (Fig. 5C). Dorsal and ventral simple chaetae not seen. Two acuminate aciculae per parapodium (Fig. 5D). Pharynx wide, though about 11 segments; pharyngeal tooth conical, inserted slightly posteriorly from anterior margin of pharynx (Fig. 5A). Proventricle long, through 12 segments, with about 30 muscle cell rows. Pygidium lost.

Remarks

Pionosyllis sp. is characterized by elongated compound chaetae, distinctly bidentate with both teeth hooked, proximal one larger than distal one, with a tendon contacting with the margin. This combination of characters is not present in any other species of the genus; however, the species is not named until more material is found.

Distribution. North West Pacific Ocean (Japan).

Subfamily Exogoninae Langerhans, 1879

Exogone naidina Örsted, 1845

Exogone naidina Örsted, 1845: 20, Figs 1-14. Hartmann-Schröder, 1971: 171, figs 56 a-c; 1979: 108, fig. 163; 1980: 56; 1981: 38; 1982: 74; 1984: 25; 1986: 45. Gardiner, 1976: 132, figs 11 j-n. San Martín, 1984: 208, pl. 46.

Exogone (Exogone) naidina San Martín, 2003: 262-265, figs 142, 143; 2005: 130-131, fig. 79.

Exogone gemmifera Fauvel, 1923: 305, figs117a-d. Day, 1967: 274, figs 12.10. p-v. Ben-

Eliahu, 1977: 78, fig. 7. Imajima, 1966c: 397, fig. 2; 1994: 108; 2001: 59; 2003: 149.

Material examined. KMNH IvR 700,161, 700,162 (2 specs) Ubara, Katsuura, Boso Peninsula; 35°07'55''N 140°17'16''E, intertidal coarse sand, sea grass and algae, coll. by E. Nishi, April 1995. KMNH IvR 700,163 (1 spec.) Ubara, Katsuura, Boso Peninsula, 35°07'55''N 140°17'16''E, intertidal rocky shore, sea grass and algae, coll. by E. Nishi, June 1996.

Distribution. Apparently cosmopolitan.

Sphaerosyllis hirsuta Ehlers, 1897

Sphaerosyllis hirsuta Ehlers, 1897: 48, pl. 3, figs 58-60; 1908: 66. Augener, 1913a: 249; 1927: 156. Fauvel, 1917: 201. Haswell, 1920b: 226. Uschakov, 1955: 190, text-fig. 55. Imajima and Hartman, 1964: 116, pl. 27, figs f-l. Imajima, 1966c: 404; 1967: 416; 1994: 108; 2003: 150. San Martín, 2005: 99-102, fig. 55A-H, 56A-H.

Sphaerosyllis hystrix Non Claparède, 1863: 45. Haswell, 1920b: 224, pl.18, figs 32-35.

Material examined. KMNH IvR 700,164 (1 spec.) Sakamoto Coast, Shizugawa, Minami-Sanriku, Sanriku coast, 38°38'11''N 141°29'03''E, intertidal rocky shore with sponges, coll. by E. Nishi, September 2003. KMNH IvR 700,165 (1 spec.) Nakagusuku Bay, Okinawajima-Island, Ryukyu Archipelago, 26º05'N 127º42'E, intertidal rocky shore with sponges, coll. by K. Tanaka, November 2003.

Distribution. Pacific Ocean (Southern Chile, Australia, Japan).

Subfamily Syllinae Grube, 1850

Genus *Alcyonosyllis* Glasby and Watson, 2001 (emended)

Alcyonosyllis Glasby and Watson, 2001: 44-45.

Type species. *Alcyonosyllis phili* Glasby and Watson, 2001.

Diagnosis

Body long with numerous chaetigers. Prostomium with two pairs of eyes, three antennae; palps fused at bases. Two pairs of tentacular cirri. Antennae, tentacular cirri, and dorsal cirri unarticulated or weakly articulated on anterior segments, becoming smooth posteriorly. Dorsal

cirri generally alternating in length. Cirrophores distinct. Ventral cirri present. Chaetal fascicles with simple hooked chaetae relatively slender, with long, thin tips and a subdistal boss, unidentate or slightly bidentate; sometimes also compound chaetae. Simple capillary ventral chaetae appearing on posterior chaetigers. Pygidium with a pair of long unarticulated cirri. Pharynx with anterior mid-dorsal tooth and 10 terminal papillae. Reproduction by schizogamous scissiparity. Ventral development of stolon.

Remarks

The genus was described with unarticulated antennae, tentacular and dorsal cirri smooth and only one kind of chaeta: simple hooked chaetae with subdistal boss. Simple chaetae with subdistal boss are present in several genera of Syllinae, such as *Haplosyllis* Langerhans, 1879; *Haplosyllides* Augener, 1924; *Parahaplosyllis* Hartmann-Schröder, 1990; *Trypanoseta* (Imajima and Hartmann, 1964), as well as in some species of *Trypanosyllis* Claparède, 1864 and *Syllis* Lamark, 1818. Several authors have suggested that the presence of these simple chaetae could be interpreted as a secondary acquisition related to a symbiotic life style with other organisms (sponges or corals) (Martín and Britayev, 1998; Musco and Giangrande, 2005). *Alcyonosyllis* differs from *Haposyllis*, *Trypanosyllis* and *Syllis* by the presence of smooth or weakly articulated dorsal cirri, from *Trypanoseta* and *Trypanosyllis* by the absence of trepan; additionally *Alcyonosyllis* differs from any of these similar genera by its chaetal shape. Simple chaetae of *Alcyonosyllis* are unidentate or slightly bidentate, distally elongated, with short small, basal spur; while in *Haplosyllis*, *Haplosyllides* and *Trypanoseta* the simple bidentate chaetae are short, proportionally thicker and more robust, with a large subdistal spur. *Parahaplosyllis* has simple chaetae with a huge, subdistal, curved spur, differing from any simple chaetae of other genera. Simple chaetae of *Trypanosyllis* are larger and thicker, generally unidentate. Finally, simple chaetae in *Syllis* are produced by a progressive fusion of blades and shafts, remaining compound on some parapodia (typically those of anterior and posterior segments). Moreover, most of these species of *Syllis* with simple chaetae have simple "ypsiloid" chaetae, which are very different from those of *Alcyonosyllis*. (The term "ypsiloid" is used to describe a thick Y-shaped chaeta produced by total or partial fusion of shaft and blade)

Alcyonosyllis exiliformis n. comb. has all the characters deffining the genus, is a

commensal of octocorals (the typical habitat of this genus), and in addition to the typical simple chaetae, it also has compound chaetae and one simple capillary ventral chaeta in posterior segments. The presence of these compound chaetae and ventral simple chaetae are considered as two additional characters in the diagnosis of the genus. Moreover, there is another interesting feature present in all the species of this genus described up to now, the development of the anterior part of stolons in ventral position. The epitokous specimens of *A. phili* Glasby and Watson, 2001 and *A. glasbyi* San Martín and Nishi, 2003 were described with a regenerating anterior tail end on the venter at the junction of the stock and stolon, comprising about 20 short segments. In addition, specimens described herein as *A. exiliformis* n. comb. were also developing stolons, which had antennae and palps in ventral position. A similar process has been observed in specimens of the genera *Trypanosyllis* and *Parahaplosyllis* (personal observations).

Alcyonosyllis is a recently described genus with only three ascribed species: *A. phili*, *A. glasbyi* and *Alcyonosyllis xaenicola* (Hartmann-Schröder, 1993). However, several authors have considered that some other species previously ascribed to other genera could actually belong to *Alcyonosyllis* (Glasby and Watson, 2001; San Martín and Nishi, 2003). Here two more species are considered to belong to this genus: *Alcyonosyllis onkylochaeta* (Hartmann-Schröder, 1991) n. comb. and *Alcyonosyllis exiliformis* (Imajima, 2003) n. comb, both with simple and compound chaetae in the same chaetal fascicle (Hartmann-Schröder, 1991b; Imajima, 2003). Other species that probably belong to *Alcyonosyllis* are: *Syllis cirrita* Lee and Rho, 1994 and *Haplosyllis bisetosa* Hartmann-Schröder, 1960, but type specimens have not been examined.

Alcyonosyllis exiliformis (Imajima, 2003) n. comb.

Figs 6, 7

Syllis exiliformis Imajima, 2003: 154-157

Material examined. MNCN 16.01/10139 (1 spec.) Ubara, Katsuura, Boso Peninsula, 35°07’55’’N 140°17’16’’E, intertidal coarse sand, sea grass and algae, coll. by E. Nishi, April 1995. MNCN 16.01/11006 (1 spec.), CBM-ZW 977 (1 spec.) Shiraiso Coast, Manazuru, Sagami Bay, 35°09’14’’N 139°08’49’’E, intertidal to subtidal rocky shore, sea grass and algae,

coll. by E. Nishi, September 2004.

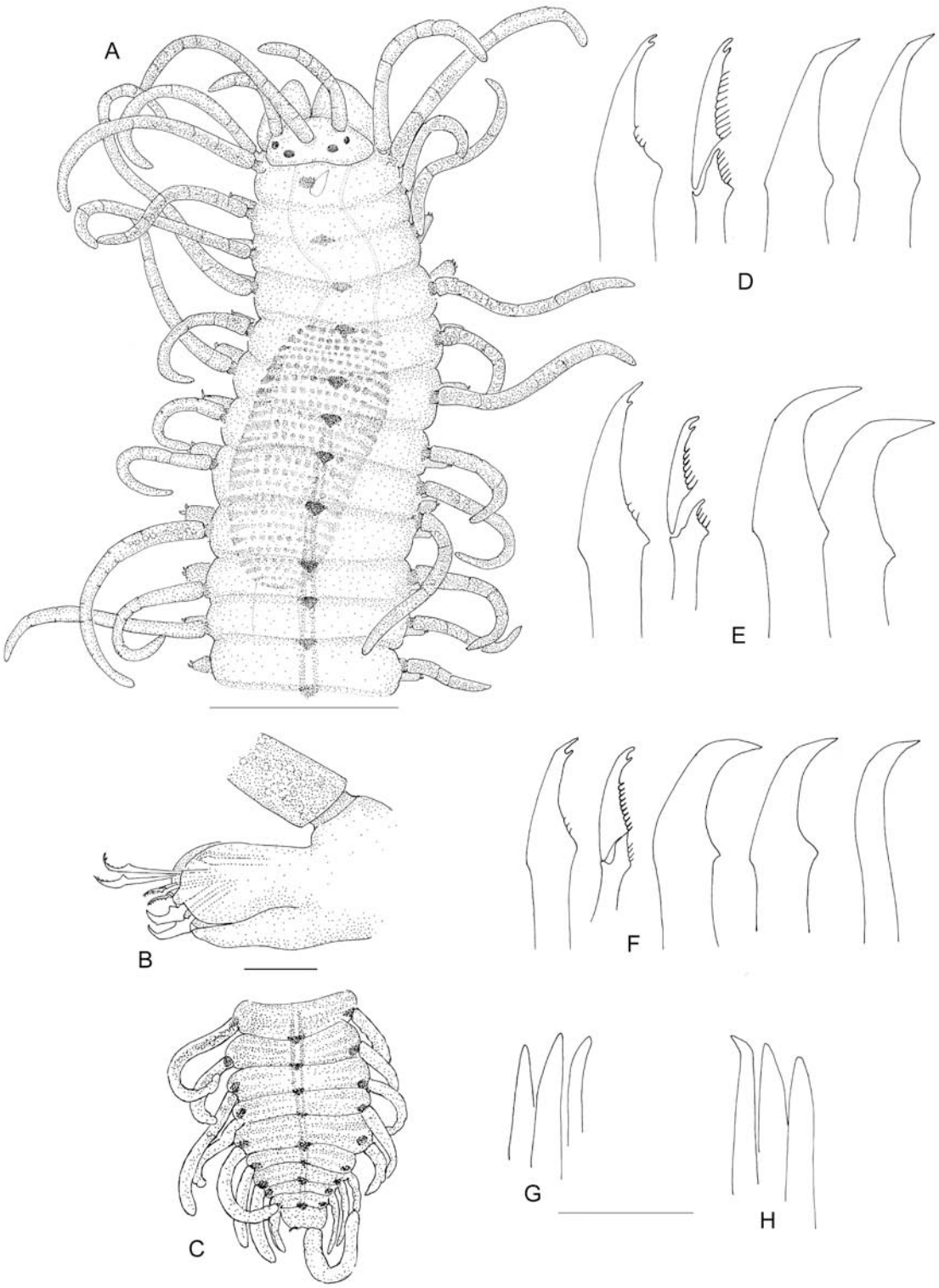

Figure 6. *Alcyonosyllis exiliformis*. CBM-ZW 977: A, Anterior end, dorsal view; B, Midbody parapodium, anterior view; C, Posterior end, dorsal view; D, Anterior chaetae; E, Midbody chaetae; F, Posterior chaetae; G, Anterior aciculae; H, Midbody and posterior aciculae. Scale: A: 0.5 mm; B: 98 µm; C: 0.4 mm; D-H: 20 µm.

Comparative material examined. *Haplosyllis xaenicola* Hartmann-Schröder, 1993: Holotype (SMF4431/1) Ternate (Molukken), Indonesia, on *Xenia viridis* Schenk, 1896.

Syllis onkylochaeta Hartmann-Schröder, 1991: Holotype (ZMH P-20222) and 3 Paratypes (ZMH P-20223) on *Xenia*, coral aquarium, Löbbecke Museum Düsseldorf (corals probably from Bali, Indonesia).

Alcyonosyllis glasbyi San Martín and Nishi, 2003: Type MNHN 1378. Shizuoka, Izu Peninsula, Japan.

Description

Longest specimen (CBM-ZW 977) 40 mm long, 0.6 mm wide, with 99 segments. Segments with median, rhomboidal dorsal area of reddish pigment and an oval to circular area on and around cirrophores (Fig. 6A). Anterior segments with posterior ring of pigment, midbody and posterior segments with four to five annuli per segment, posterior one more distinct. Prostomium broader than long, rectangular to oval with two pairs of eyes in trapezoidal arrangement, posterior ones larger than anterior pair. Palps broad, fused basally, longer than prostomium. Median antenna inserted on middle of prostomium, slightly pseudoarticulated, approximately twice longer than lateral antennae. Lateral antennae inserted on anterior margin of prostomium, pseudoarticulated, slightly longer than combined length of prostomium and palps (Fig. 1A). Peristomium similar to subsequent segments. Dorsal tentacular cirri pseudoarticulated, similar in length to median antennae; longer than ventral pair. Dorsal cirri of anterior part of body slightly pseudoarticulated (Fig. 6A), midbody and posterior cirri smooth (Figs 6B, C). Dorsal cirri of first to third chaetigers long, similar in length to dorsal tentacular cirri. Subsequent cirri alternating in length, longest similar in length to segment width, shortest about two-third of their length (Fig. 6A). Longer dorsal cirri pointing up and shorter ones pointing down. Distinct cirrophores present on all chaetigers (Fig. 6B). Ventral cirri digitiform, not exceeding beyond tips of parapodia. Parapodia with pre- and postchaetal lobes, similar in length, with a distal rounded papilla on prechaetal lobe (Fig. 6B). Anterior parapodia with three kinds of chaetae, one to two bidentate simple chaetae dorsally located with short and thin spines on margin, one to two bidentate compound chaetae with short blades (26 μm), long spines on margin and distal spines on fangs; and two hooked unidentate simple chaetae with strongly enlarged tip and smooth margin (Figs 6D; 7A, B). Midbody chaetigers with

same kind and number of chaetae but compound chaetae with slightly shorter blades (18 μm) and unidentate simple chaetae with distal tip longer and more curved (Figs 6E; 7C). Posterior segments with same number and kind of midbody chaetae plus a fourth kind of chaeta: ventral simple capillary chaeta, straight and distally curved, without subdistal boss (Figs 6F; 7D). Three aciculae per parapodium, two straight and distally pointed, one thinner and distally blunt (Figs 6G, H). Pygidium conical, two smooth anal cirri, similar in length to dorsal cirri (Fig. 6C). Pharynx through four segments, narrower than proventricle, provided with one conical distal tooth located in anterior part (Fig. 6A). Proventricle extending through six segments, with about 30 rows of muscle cells (Fig. 6A). Specimen CBM-ZW 977 developing female stolon with antennae and growing palps located in ventral position, with 18 segments.

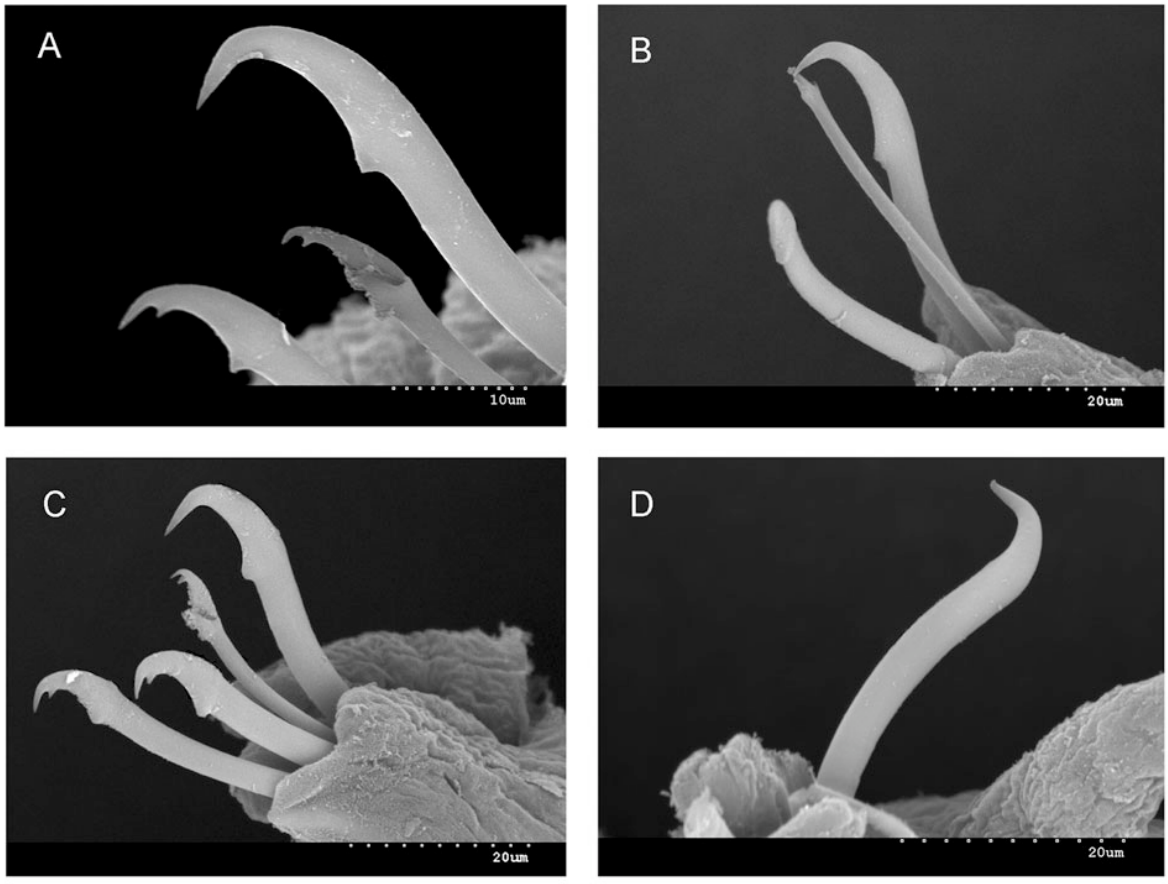

Figure 7. *Alcyonosyllis exiliformis*. SEM. MNCN 16.01/11006: A, B, Midbody chaetae; C, Midbody chaetae; D, Ventral capillary chaeta, posterior segment.

Remarks

This species is considered to belong to the genus *Alcyonosyllis* since it has weakly articulated dorsal cirri, becoming smooth towards the posterior part of the body, conspicuous cirrophores and simple hooked chaetae with subdistal boss. Besides, it is also a commensal with some species of corals (the typical habitat associated with this genus) and develops stolons in a ventral position. Additionally, *A. exiliformis* has compound chaetae and a fourth kind of chaeta on posterior chaetigers, which may be interpreted as ventral capillary chaetae. Dorsal and ventral capillary chaetae are present in most of the genera of Syllidae but had not been previously described for *Alcyonosyllis*. This kind of chaeta is commonly distally curved, and there is only one located in the most dorsal position of the chaetal fascicle and/or in the most ventral position. Both, dorsal and ventral simple capillary chaetae usually occur only on posterior segments of adult specimens. *Alcyonosyllis exiliformis* has ventral chaetae because they only occur in the posterior part of the body of long specimens, there is only one per chaetal fascicle always in the most ventral position, and it does not have a subdistal boss. Simple ventral chaetae might also be present in other species of the genus.

This species is associated with the gorgonaceans *Acalycigorgia inermis* (Hedlund, 1890), (cream-yellow colour) and *Anthoplexaura dimorpha* (Kükenthal, 1908) (light-orange). Types associated with *Verucella* sp. (Imajima, 2003).

Distribution. North West Pacific Ocean (Japan).

***Branchiosyllis exilis* (Gravier, 1900)**

Syllis (Typosyllis) exilis Gravier, 1900: 160, figs. 28-30. Augener, 1913a: 192. Fauvel, 1953: 151-152, fig. 75. Day, 1967: 250, fig. 12.4h-j.

Branchiosyllis exilis Westheide, 1974: 60-64, fig. 26. Hartmann-Schröder ,1986: 37; 1991a: 24, figs. 14-18. Capa *et al.*, 2001: 105. San Martín, 2003: 332, figs. 184, 185. San Martín *et al.*, in press.

Material examined. CBM-ZW 978 (3 specs) Ubara, Katsuura, Boso Peninsula, 35°07’55’’N 140°17’16’’E, intertidal rocky shore, sea grass and algae, coll. by E. Nishi, June 1996. CBM-ZW 979 (1 spec.) Nakagusuku Bay, Okinawajima-Island, Ryukyu Archipelago, 26º05’N 127º42’E, intertidal rocky shore with sponges, coll. by K. Tanaka, November 2003.

Comparative material examined. Polytype MNHN 158. Djibouti, Gulf of Aden. MNCN16.01/198, 6551, 751 (Several specimens) Mediterranean Sea; identified by San Martín (2003). AM W30095 (4 specs) Western Astralia, Kimberley region Bernouli Is. 15° S, 124° 47' E, sandy substratum with coral rubble, intertidal, coll. P.A. Hutchings, 12 Jul 1988. AM W30096 (8 specs) Reef S of Lucas Is., Brunswick Bay, 15° 16' S, 124° 29' E, dead coral and *Sargassum* with heavy silt loading, 2m, coll. P.A. Hutchings, 24 July 1988; identified by San Martín *et al.* (in press).

Branchiosyllis maculata (Imajima, 1966). AM W30108 (4 specs) Western Australia, inshore reef off Ned's Camp, Cape Range National Park, 21° 59' S, 113° 59' E, frilly Caulerpa sp., 1m, 2 Jan 1984. AM W30109 (2 specs) Western Australia, N end of beach, Bundegi Reef, Exmouth Gulf, 21° 49' S, 114° 11' E, rocky rubble with sediment, brown alga with epiphytic growth, intertidal, 4 Jan 1984. AM W30111 (2 specs) Western Australia, N end of beach, Bundegi Reef, 21° 49' S, 114° 11' E, rocky rubble and coralline algae with green epiphytes, 2m, 4 Jan 1984; identified by San Martín *et al.* (in press). ZMA V.Pol. 5259 (2 specs) Indonesia, NE coast of Sumba, 09°57'S 120°49'E, 45 m, sandy bottom and sponges, Snellius II Expedition, 16.09.1984; identified by Aguado, San Martín and Ten Hove (in press).

Description

Body cylindrical dorsally. Prostomium oval to pentagonal, four eyes in trapezoidal arrangement. Median antenna inserted between anterior pair of eyes, lateral antennae inserted near anterior margin of prostomium, shorter than median antenna. Palps similar in length to prostomium. Peristomium shorter than subsequent segments. Dorsal tentacular cirri longer than median antenna, ventral ones shorter than dorsal tentacular cirri. Dorsal cirri of chaetiger 1 long, subsequent dorsal cirri alternating long and short. Parapodial lobes conical, distally bilobed, postchaetal lobes longer than prechaetal. Ventral cirri digitiform, shorter than parapodial lobes. Compound heterogomph chaetae on anterior parapodia, blades falcigerous, bidentate, with short spines. Progressively along body, chaetae with some blades becoming unidentate and smooth on margin; from midbody onwards some chaetal blades rotated 180º, becoming claw-shaped; number of claw-shaped chaetae increasing and non-modified chaetae decreasing posteriorly. Posterior parapodia with only claw-shaped chaetae, larger ventrally.

Anterior parapodia with two slender aciculae, one straight and one with tip slightly oblique; from midbody posteriorly, single acicula on each parapodium, thicker than anterior ones, distally oblique. Pharyngeal tooth located anteriorly on the pharynx. Proventricle longer than pharynx. Pygidium small, with two anal cirri similar in shape and length to dorsal cirri.

Remarks

Branchiosyllis maculata has already been reported from Japan by Imajima (1966); it is easily recognizable by the dark spots on some articles of the dorsal cirri. The specimens studied lacked dark spots on the dorsal cirri, which are shorter than those of *B. maculata*, and broadly coincide with material of *B. exilis* examined from Australia and Mediterranean Sea. A revision of the material identified as *B. exilis* from around the world is necessary since it might actually be a complex of species.

Distribution. Apparently circumtropical, also present in the Mediterranean Sea.

Opisthosyllis longocirrata Monro, 1939

Opisthosyllis longocirrata Monro, 1939: 389-390, fig. 300. Fauvel, 1953: 154-155, fig. 77. Imajima, 1966d: 228-230, fig. 41. Hartman, 1974: 616.

Material examined. CBM-ZW 980 (1 spec.) Zampa Cape, Okinawajima Island, Ryukyu Archipelago, 26°26’04’’N E141°29’03’’, 1-3 m, coral reef, coll. by E. Nishi, April 1995.

Distribution. Red Sea, Indian Ocean (Maldives Islands), Pacific Ocean (Tahiti Island, Japan).

Syllis alternata Moore, 1908

Syllis alternata Moore, 1908: 323. Berkeley and Berkeley, 1938: 37-38, fig. 3; 1948: 77, fig. 115. Rioja, 1941: 691-692, pl. 3, figs 1-9. Capa *et al.*, 2001: 106. San Martín, 2003: 354-358, figs 192, 193.

Syllis (Typosyllis) alternata Hartman, 1968: 479, figs 1-5.

Typosyllis alternata Imajima, 1966e: 273-275, fig. 58; 1994: 110; 1997: 175; 2001: 61; 2003: 163-164; 2005: 84; 2006: 355. Kudenov and Harris, 1995: 83-85, fig. 1.32. Licher, 1999: 253-255, fig.106.

Material examined. CBM-ZW 981 (1 spec.) Bise Beach, Motobu, Okinawajima Island,

Ryukyu Archipelago, 26º28'N 128º35'E, intertidal sea grass, coll. by E. Nishi, January 1996.

Distribution. Atlantic Ocean (U.S.A.), Mediterraneann Sea, North Pacific Ocean (from Alaska to Panama, Japan), Indian Ocean (Indonesia).

Syllis armillaris (Müller, 1771)

Nereis armillaris Müller, 1771: 150.

Typosyllis armillaris Hartman, 1968: 481, figs 1-5. Licher, 1999: 189-199, fig. 84.

Syllis (Typosyllis) armillaris Fauvel, 1923: 264-265, fig. 99a-f. Hartmann-Schröder, 1971: 149-150, fig. 50.

Syllis armillaris Berkeley and Berkeley, 1948: 72, fig. 104. Capa *et al.*, 2001: 106. San Martín, 2003: 423-426, figs 232, 233. Musco and Giangrande, 2005: 472-473, fig. 4.

Material examined. CBM-ZW 982 (1 spec.) Bise Beach, Motobu, Okinawajima Island, Ryukyu Archipelago, 26º28'N 128º35'E, intertidal sea grass, coll. by E. Nishi, January 1996. CBM-ZW 983 (1 spec.) Ubara, Katsuura, Boso Peninsula, 35°07'55''N 140°17'16''E, intertidal rocky shore, sea grass and algae, coll. by E. Nishi, April 1998. CBM-ZW 984 (1 spec.) Odawa, Yokosuka, Sagami Bay, 35°12'52''N 139°37'10''E, 5-10 m, sandy bottom, sea grass and algae, coll. by T. Kudo, May 2002. CBM-ZW 985 (4 specs) Sakamoto Coast, Shizugawa, Minami-Sanriku, Sanriku coast, 38°38'11''N 141°29'03''E intertidal rocky shore with sponges, coll. by E. Nishi, September 2003. CBM-ZW 986 (3 specs) Nakagusuku Bay, Okinawajima-Island, Ryukyu Archipelago, 26º05'N 127º42'E, intertidal rocky shore with sponges, coll. by K. Tanaka, November 2003.

Distribution. Apparently cosmopolitan.

Syllis ehlersioides (Marenzeller, 1890)

Typosyllis ehlersioides Marenzeller, 1890: 4-5, fig. 2. Imajima, 1966e: 279-282, fig. 266; 1967: 421; 2003: 165; 2006: 355. Licher, 1999: 199.

Syllis ehlersioides Augener, 1913b: 254-255.

Material examined. CBM-ZW 988 (1 spec.) Shiraiso Coast, Manazuru Peninsula, Sagami Bay, 35°09'14''N 139°08'49''E, intertidal to subtidal rocky shore, sea grass and algae, coll. by E. Nishi, May 2002. CBM-ZW 989 (1 spec.) Nakagusuku Bay, Okinawajima-Island,

Ryukyu Archipelago, 26º05'N 127º42'E, intertidal rocky shore with sponges, coll. by K. Tanaka, November 2003. MNCN ADN 9606 (1 spec.) Shiraiso Coast, Manazuru, Sagami Bay, 35°09'14''N 139°08'49''E, intertidal to subtidal rocky shore, sea grass and algae, coll. by E. Nishi, September 2004, fixed and preserved in 95% ethanol.

Distribution. North West Pacific Ocean (Bering Sea, Okhotsk Sea, Japan, Korea).

Syllis gracilis Grube, 1840

Syllis gracilis Grube, 1840: 77. Monro, 1933: 30. Fauvel, 1953: 147-148, fig. 73f-i. Hartman, 1968: 463, figs 1-4. Imajima, 1966e: 247-248, fig. 49; 2003: 157. Licher, 1999: 289-291, fig. 10A. Capa *et al.*, 2001: 111-112. San Martín, 2003: 413-416, figs 226, 227.

Material examined. CBM-ZW 990 (2 specs) Nakagusuku Bay, Okinawajima-Island, Ryukyu Archipelago, 26º 05'N 127º 42'E, intertidal rocky shore with sponges, coll. by K. Tanaka, November 2003.

Distribution. Apparently cosmopolitan.

Syllis hyalina Grube, 1863

Typosyllis hyalina Grube, 1863: 45, pl. 4, fig. 8. Imajima, 1966e: 271-273, fig. 57; 1967: 420; 2005: 84. Hartman, 1968: 487-488, figs 1-3. Kudenov and Harris, 1995: 87-89, fig. 1.34. Licher, 1999: 199-205, fig. 86.

Syllis hyalina Monro, 1933: 30. Berkeley and Berkeley, 1948: 74, fig. 107-108. Capa *et al.*, 2001: 112. San Martín, 1984: 387-390, fig. 101; 2003: 426-429, figs 234, 235.

Material examined. CBM-ZW 991 (1 spec.) Tokyo Bay to Uraga Channel, 35°09'18''N 139°47'51''E, 79 m, rocky shore, coll. by E. Nishi, November 1995. MNCN 16.01/10999 (1 spec.) Shiraiso Coast, Manazuru, Sagami Bay, 35°09'14''N 139°08'49''E, intertidal to subtidal rocky shore, sea grass and algae, coll. by E. Nishi, September 2004, fixed and preserved in 95% ethanol.

Distribution. Apparently cosmopolitan in warm and tropical seas.

Syllis marugani Aguado, San Martín and Nishi, 2006

Syllis marugani Aguado, San Martín and Nishi, 2006: 12-15.

Material examined. MNCN ADN 9614 (2 specs) Shiraiso Coast, Manazuru, Sagami Bay, 35°09'14''N 139°08'49''E, intertidal to subtidal rocky shore, sea grass and algae, coll. by E. Nishi, September 2004,

Distribution. North West Pacific Ocean (Japan).

Syllis monilata (Imajima, 1966) n. comb.

Typosyllis monilata Imajima, 1966e: 287-288, fig. 63; 1967: 421. Licher, 1999: 119-121, fig. 55.

Syllis torquata Non Marion and Bobretzky, 1875: 20-24, pl.1, fig. 5a, pl. 2, fig. 5. Fauvel, 1934: 306-307.

Material examined. MNCN ADN 9615 (1 spec.) Shiraiso Coast, Manazuru, Sagami Bay, 35°09'14''N 139°08'49''E, intertidal to subtidal rocky shore, sea grass and algae, coll. by E. Nishi, September 2004, fixed and preserved in 95% ethanol.

Distribution. North West Pacific Ocean (Japan).

Syllis multiannulata n. sp.

Figs 8-11

Material examined. Holotype MNCN 16.01/10997 and paratypes (5 specs) MNCN 16.01/10998. Shiraiso Coast, Manazuru, Sagami Bay, 35°09'14''N 139°08'49''E, intertidal to subtidal rocky shore, sea grass and algae, coll. by E. Nishi, September 2004, fixed and preserved in 95% ethanol. MNCN 16.01/11001 (16 specs). Shiraiso Coast, Manazuru, Sagami Bay, 35°09'14''N 139°08'49''E, intertidal to subtidal rocky shore, sea grass and algae, coll. by E. Nishi, September 2004, fixed and preserved in 95% ethanol.

Comparative material examined. *Syllis corruscans* Haswell, 1886. AM W31405 (7 specs) Australia, New South Wales, Jervis Bay, Darling Road, near anchorages, 35°07'18"S 150°44'06"E, 18 m, 23 Jan 1973; identified by San Martín, Hutchings and Aguado (unpublished data).

Syllis inflata Marenzeller, 1879. AM W28225 (4 specs) Australia, Victoria, Corio Bay, Port

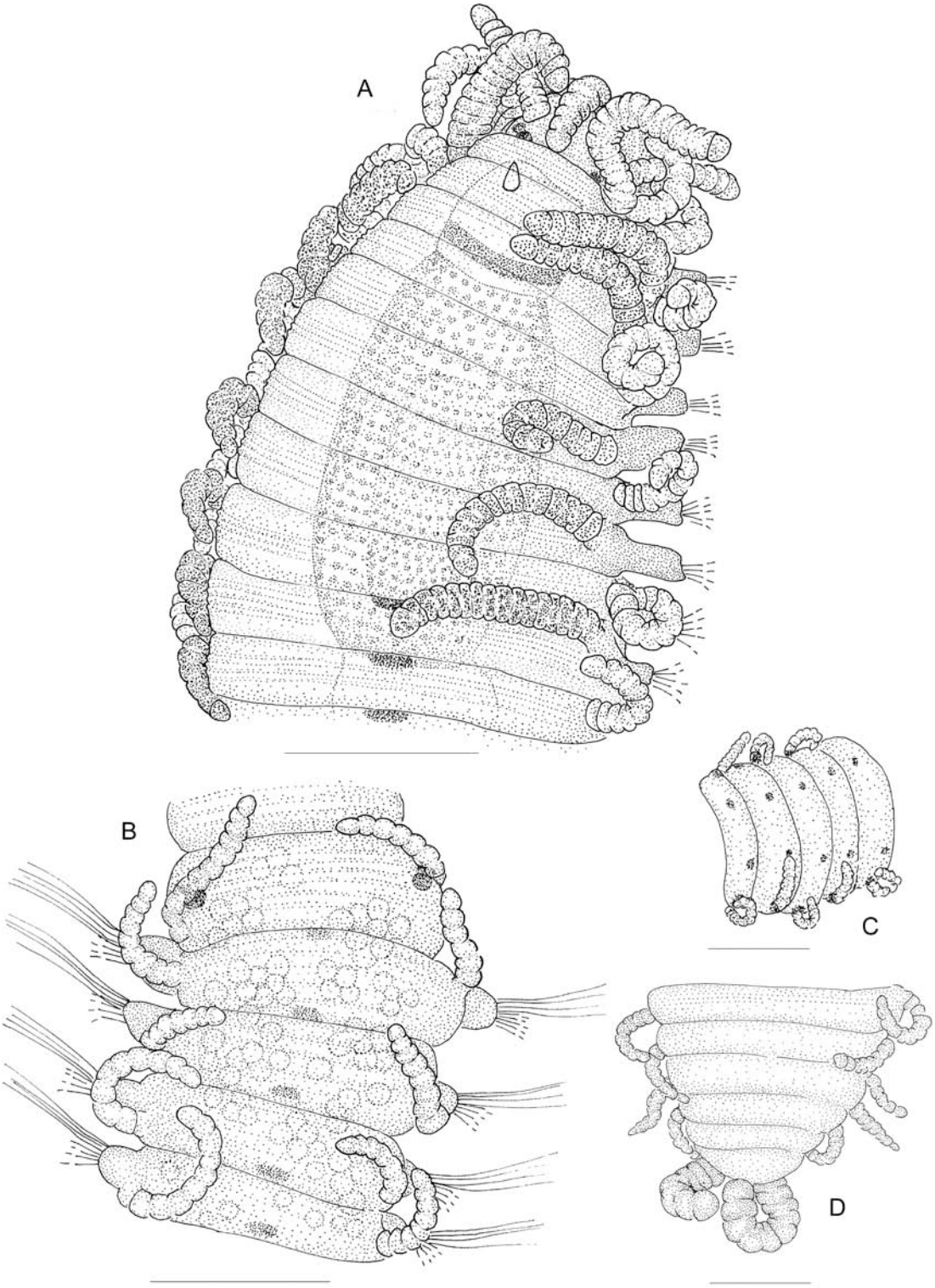

Figure 8. *Syllis multiannulata* n. sp.: A, Anterior end, dorsal view, holotype MNCN 16.01/10997; B, Stolon, dorsal view, paratype MNCN 16.01/10998; C, Midbody segments, paratype MNCN 16.01/10998; D, Posterior end, dorsal view, paratype MNCN 16.01/10998. Scale A: 0.5 mm; B, C, D: 0.2 mm.

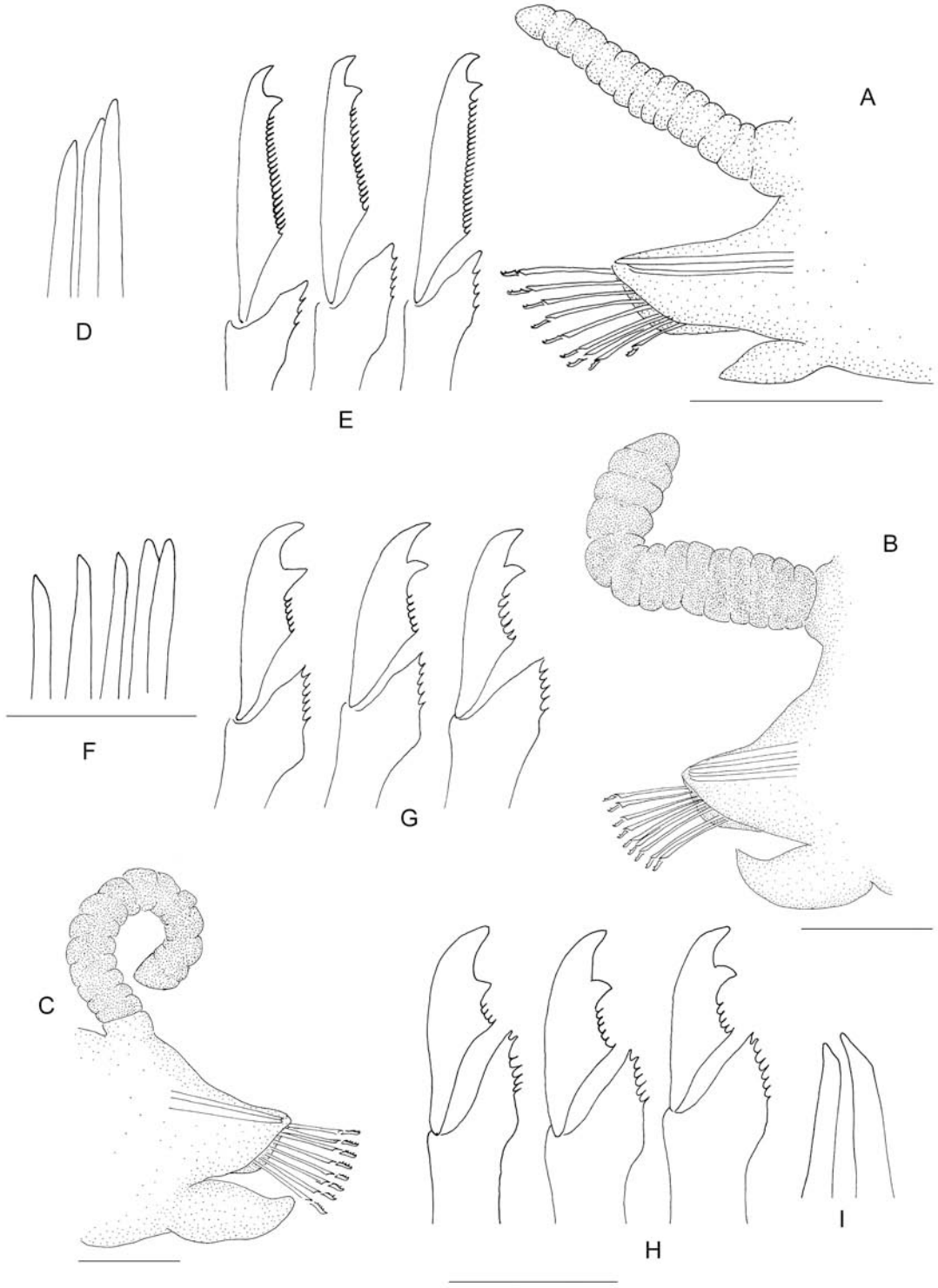

Figure 9. *Syllis multiannulata* n. sp. Holotype MNCN 16.01/10997: A, Anterior parapodium, anterior view; B, Midbody parapodium, anterior view; C, Posterior parapodium, anterior view; D, Anterior aciculae; E, Anterior chaetae; F, Midbody aciculae; G, Midbody chaetae; H, Posterior chaetae; I, Posterior aciculae. Scale A: 0.2 mm; B, C: 98 µm; D, F, I: 48 µm; E, G, H: 20 µm.

Phillip Bay, 38°05'02"S 144°23'47"E, silty clay, 9 m, 11 Feb 1987; identified by San Martín, Hutchings and Aguado (unpublished data).

Syllis heterosetosa (Hartmann-Schröder, 1991). AM W27573 (1 spec) Australia. New South Wales, Montagu Roadstead, Jervis Bay, 35°02'12"S 150°46'E, 3 Jun 1991. AM W17558 (1 spec.) Australia, Jervis Bay, off Cararma Creek, Hare Bay, 35° 00' 30"S, 150° 46'E, Posidonia, muddy sand, 18 Oct 1972; identified by San Martín, Hutchings and Aguado (unpublished data).

Description

Holotype mature (Fig. 8A), with 120 segments, 17 mm long, 1 mm wide. Longest paratype with 95 segments, 16 mm long, 1 mm wide, with stolon (probably male) of 24 segments (Fig. 8B). Body broad, thick and strongly cylindrical, ventrally flattened. Segments secondarily ringed, with three to five rings. Body pigmented in orange with anal and some dorsal cirri coloured red. Some specimens with dark, red spots on middle of midbody and posterior segments (Figs 8A, B); smaller specimens with prostomium and anterior segments markedly orange-reddish, red spots on the cirrophores and organized in two longitudinal lines on dorsum of midbody to posterior segments (Fig. 8C). Dark transversal band on posterior part of pharynx, visible by transparency in third chaetiger (Fig. 8A). Antennae, tentacular, anal and dorsal cirri weakly articulated, rough in appearance, more distinctly articulated in smaller specimens. Prostomium wider than long, partially covered by peristomium, with two pairs of distinct red eyes very close each other, in trapezoidal arrangement (Fig. 8A). Median antenna broad, arising from middle of prostomium, longer than combined length of prostomium and palps, with 12-14 articles; lateral antennae shorter than median one, inserted on anterior margin of prostomium, with eight to nine articles. Palps broad, slightly longer than prostomium, ventrally folded (Fig. 10B). Peristomium shorter than subsequent segments, with two pairs of tentacular cirri. Dorsal tentacular cirri broad, with 19-20 articles, ventral ones with 12-14 pseudoarticles (Figs 8A; 10A). Dorsal cirri broad, with granular material inside, alternating in orientation and insertion. Some cirri longer, with 16 pseudoarticles, curving over dorsum, more dorsally inserted and strongly coloured red. Shorter cirri with 14 pseudoarticles, curving also dorsally but more ventrally inserted and coloured orange (Figs 8A; 10A, C, D). Cirrophores present. Ventral cirri short, conical on anterior segments and lanceolate on

midbody to posterior segments, not extending beyond parapodial lobes, becoming wider towards posterior segments (Figs 9A-C). Parapodial lobes present, prechaetal lobe shorter than postchaetal one (Figs 9A-C). Anterior parapodia each with 17 compound, heterogomph chaetae, distal part of shafts provided with spines and bidentate blades (about 31 µm length), distal tooth curved, larger than proximal one, with thin spines on margin (Figs 9E; 10E, F). Midbody chaetigers with 12-13 compound chaetae, shafts with spines, blades shorter (26 µm length), with distal tooth larger than proximal one; and short spines on margin (Figs 9G; 11A, B). Posterior parapodia with about 12 compound chaetae, with spinulated shafts; blades similar in length to those of midbody (25-26 µm), provided with two large distal teeth, distal one larger than proximal one, and three to five thin, short spines on margin (Figs 9H; 11C, D). Anterior parapodia with three straight and pointed aciculae (Fig. 9D); midbody parapodia with three to five aciculae, some slightly bent and acuminate (Fig. 9F); posterior parapodia with two aciculae, one distally bent (Fig. 9I). Pygidium conical, with two broad anal cirri, longer than pygidium and last segment together, with eight to nine articles (Fig. 8D). Pharynx extending through two to three segments; conical tooth on anterior margin; anterior papillae not seen. Proventricle long, extending through seven segments, with about 28 cell-rows (Fig. 8A).

Remarks

Syllis multiannulata n. sp. is principally characterized by the presence of annulated segments, antennae and cirri weakly articulated, dorsal cirri originating from different levels and parapodia with pre- and postchaetal lobes. Another interesting character is the considerably short pharynx, which is markedly shorter than the proventricle. There are only three other species of *Syllis* sharing these characters: *Syllis corruscans* Haswell, 1886, *Syllis inflata* Marenzeller, 1879 and *Syllis heterosetosa* (Hartmann-Schröder, 1991a). However, they differ in having long blades (pseudospiniger-like chaetae) while the blades of *S. multiannulata* n. sp. are all short falcigerous. Also, *S. corruscans* and *S. inflata* show a clear alternation pattern in the length of dorsal cirri, whose articulations are, in some cases, almost nonexistent. *Syllis inflata* and *S. heterosetosa* have blades of compound chaetae with long spines distally, which reach the level of the proximal tooth (Haswell, 1886; Marenzeller, 1879; Hartmann-Schröder, 1991a). Moreover, *S. multiannulata* n. sp. has a dark red ring of colour in the pharynx, visible

by transparency, which is not seen in any of these similar species. Some authors, such as

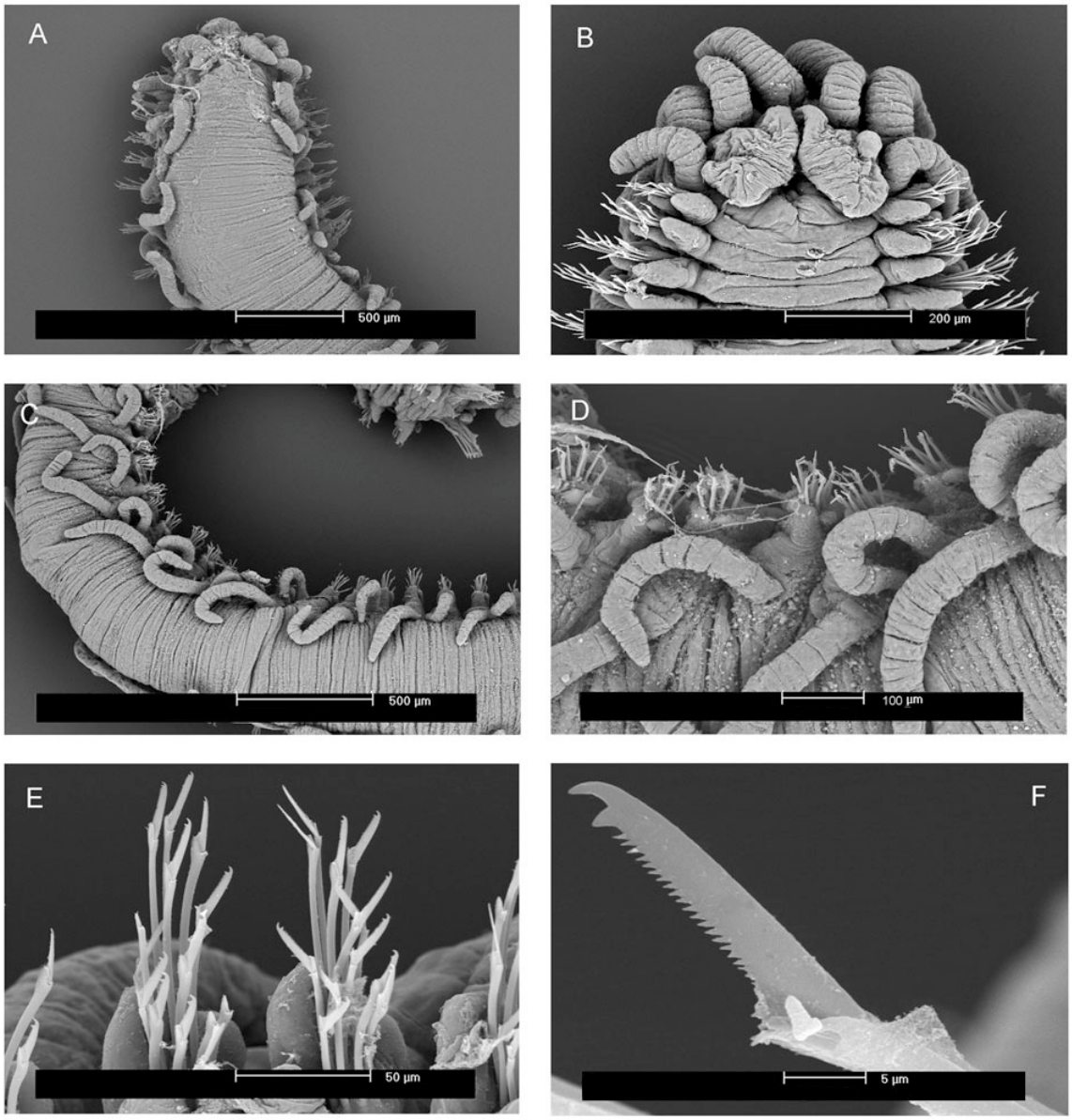

Figure 10. *Syllis multiannulata* n. sp. SEM. MNCN 16.01/11008: A, Anterior end, dorsal view; B, Anterior end, ventral view; C, D, midbody, dorsolateral view; E, Anterior chaetae; F, Anterior chaeta.

Haswell (1886, 1920a) and Licher (1999) have suggested that there are clear differences between these species and the rest of the species considered to belong to *Syllis*, although they found similarities with some genera of Eusyllinae, principally due to the presence of pseudoarticulated to unarticulated cirri. However, reproduction by schyzogamy, observed in

S. corruscans, S. inflata (Haswell, 1886, 1920a; personal observations on material from Australia), and in *S. multiannulata* n. sp., might suggest that these species are closer evolutionarily to other species currently placed in Syllinae but might constitute a group that evolved differently from the rest of the species of *Syllis*. A revision of these four species is in preparation by the first two authors in order to stablish their relationships with the Syllinae and with members of the Eusyllinae.

Distribution. North West Pacific Ocean (Japan).

Etymology. The name refers to the segments with several annuli.

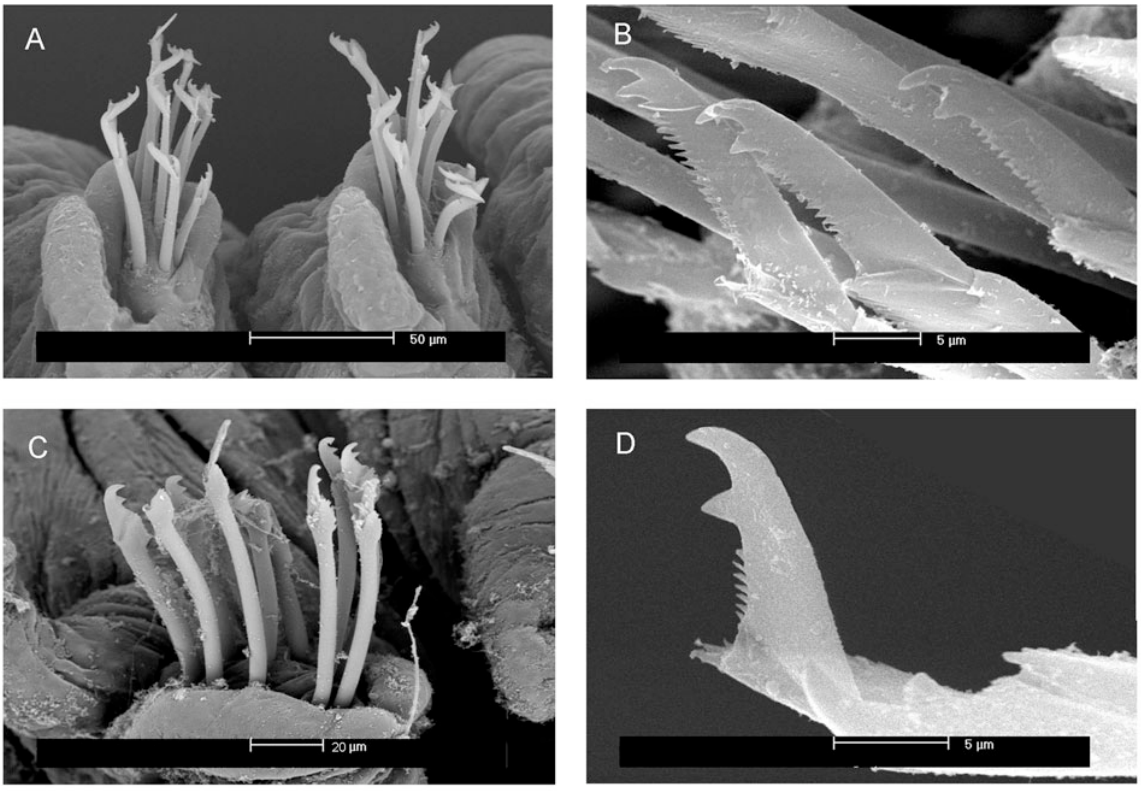

Figure 11. *Syllis multiannulata* n. sp. SEM. MNCN 16.01/11008: A, B, Midbody chaetae; C, D, Posterior chaeta.

Syllis nipponica (Imajima, 1966) n. comb.

Typosyllis nipponica Imajima, 1966e: 266-268, fig. 57; 1967: 420; 1994: 109; 2003: 165-166. Licher, 1999: 121-124.

Material examined. CBM-ZW 992 (2 specs) Shiraiso Coast, Manazuru, Sagami Bay,

35°09’14’’N 139°08’49’’E, intertidal to subtidal rocky shore, sea grass and algae, coll. by E. Nishi, May 2002. CBM-ZW 997 (1 spec.), MNCN16.01/11007 (1 spec.) Mangokuura, Ishinomaki, Sanriku coast, 39º02’N 141º51’E intertidal coarse sand, coll. by E. Nishi, June, 2002.

Distribution. North West Pacific Ocean (Japan, Okhotsk Sea, Yellow Sea).

Syllis okadai Fauvel, 1934

Syllis okadai Fauvel, 1934: 307-309, figs1, 2.

Syllis (Typosyllis) okadai Fauvel, 1953: 152-153, fig. 76.

Typosyllis okadai Imajima and Hartman, 1964: 137. Imajima, 1966e: 269-270, fig. 56. Lee and Rho, 1996: 271-273, fig. 3. Licher, 1999: 248-250.

Material examined. CBM-ZW 994 (2 specs) Shiraiso Coast, Manazuru Peninsula, Sagami Bay, 35°09’14’’N 139°08’49’’E, intertidal to subtidal rocky shore, sea grass and algae, coll. by E. Nishi, May 2002. MNCN ADN 9617 (4 specs) Shiraiso Coast, Manazuru, Sagami Bay, 35°09’14’’N 139°08’49’’E, intertidal to subtidal rocky shore, sea grass and algae, coll. by E. Nishi, September 2004, fixed and preserved in 95% ethanol.

Distribution. Indian Ocean (Camboya, Adaman Islands). North West Pacific Ocean (Japan).

Syllis pectinans Haswell, 1920

Syllis (Typosyllis) pectinans Haswell, 1920a: 93-94, pl. 10, figs 3-6.

Typosyllis pectinans Hartmann-Schröder, 1965: 287-288. Licher, 1999: 229-233, fig. 97.

Typosyllis (Typosyllis) lincolnensis Hartmann-Schröder, 1985: 67, figs 7-10; 1986: 39; 1987: 34; 1989: 20-21; 1990: 47

Opisthosyllis brunnea Non Langerhans, 1879: 541. Imajima, 1966d: 230-233, fig. 42 a-n.

Material examined. CBM-ZW 995 (1 spec.) Shikine Island, Izu-Ogasawara Archipelago, 34º47’N 139º 23’E, intertidal rocky shore, coll. by M. Mitsuhashi, February 1996.

Remarks

This species is characterized by having compound chaetae with short, unidentate blades, provided with distinct, long spines on margin, all blades of similar length, and a pharyngeal tooth located on anterior half of pharynx, far from the anterior ring. Imajima (1966d) described

some specimens as *O. brunnea*, which perfectly agree with the description of *S. pectinans*. *Opisthosyllis brunnea* has an occipital flap, the pharyngeal tooth is located near the posterior end of the pharynx, and the compound chaetae of posterior parapodia are almost smooth, with distinctly enlarged distal tooth. For these reasons, we consider that the report of *O. brunnea* from Japan by Imajima (1966d) corresponds to *S. pectinans*.

Distribution. Indian Ocean (Australia), South Pacific Ocean (Chile, Australia, Japan).

Syllis pigmentata (Chamberlin, 1919) n. comb.

Pionosyllis pigmentata Chamberlin, 1919: 7-8.

Typosyllis pigmentata Licher, 1999: 233-235, fig. 98.

Typosyllis fasciata Non *Syllis fasciata* Malmgren, 1867: 161-162, pl. 8, fig. 47, pl. 9, fig. 52. Imajima, 1963: 353; 1966e: 276, fig. 245. Imajima and Hartman, 1964: 135-136, pl. 33, figs j-o.

Material examined. MNCN ADN 9607 (1 spec.) Shiraiso Coast, Manazuru, Sagami Bay, 35°09’14’’N 139°08’49’’E, intertidal to subtidal rocky shore, sea grass and algae, coll. by E. Nishi, September 2004, fixed and preserved in 95% ethanol.

Remarks

The specimen agrees with those described from Japan by Imajima (1963, 1966b) and Imajima and Hartman (1964) as *S. fasciata* Malmgren, 1867. These specimens were later identified by Licher (1999) as *Typosyllis pigmentata* (Chamberlin, 1919). *Typosyllis* and *Syllis* have been considered synonyms (San Martín, 1984, 1992, 2003), hence this species is reported herein as a new combination of *Syllis*.

Distribution. North West Pacific Ocean (from Russia to South China). North East Pacific Ocean (Mexico).

Syllis pilosa n. sp.

Fig. 12

Material examined. Holotype MNCN 16.01/10141 and Paratype MNCN 16.01/10142 Tokyo Bay to Uraga Channel, 35°09’18’’N 139°47’51’’E, 79m, rocky shore, coll. by CMNH, November 1995.

Description

Holotype a complete specimen in two fragments, anterior one with 53 segments, 1.8 mm long, and posterior one with 39 segments, 0.6 mm long and 0.6 mm wide. Paratype complete, 1.2 mm long, 0.6 mm wide, for 72 segments. Body long, colourless to white, except dorsal cirri, which contain yellowish fibrillar material. Two distinct transversal rows of cilia on dorsum of each segment (Fig. 12A). Prostomium oval, broader than long, with two pairs of small eyes in trapezoidal arrangement, anterior pair larger than posterior. Palps longer than prostomium, almost twice as long, triangular, fused at base. Median antenna arising from middle of prostomium, shorter than combined length of prostomium and palps together, with 15 articles; lateral antennae inserted on anterior margin of prostomium, similar in length to median one, with 12-17 articles. Peristomium similar in length to subsequent segments, with two pairs of tentacular cirri, dorsal ones with 17 articles, slightly longer than ventral ones, with 12 articles (Figs 12A, B). Dorsal cirri slightly longer than parapodia, with 10-13 articles, without distinct alternation in length. Ventral cirri conical and short, not extending beyond parapodial lobes (Fig. 12D). Parapodia each with compound chaetae gradually shorter towards posterior region of body. Anterior chaetigers with five to six long chaetae (pseudospinigers) (104-80 µm length), and eight to 12 falcigers with blades decreasing dorsoventrally in length from dorsal (44 µm) to ventral (37 µm); all chaetae bidentate (Fig. 12E). Chaetae gradually becoming more distinctly bidentate through posterior part of body, holotype with compound chaetae clearly bidentate from chaetigers 10-11. Midbody chaetigers with bidentate compound chaetae: two longer (pseudospinigers) (84 µm length), and six to seven falciger chaetae dorsoventrally decreasing in length from dorsal (40 µm) to ventral (22 µm) (Fig. 12F). Posterior chaetigers with one or two clearly bidentate pseudospinigers (70 µm length) and six to seven falciger chaetae noticeably bidentate, gradually decreasing in length from dorsal (51µm) to ventral (19 µm) (Fig. 12G). Three last segments only with one shorter pseudospiniger chaeta. Posterior chaetigers with one conspicuosly bidentate dorsal simple chaeta (Fig. 12K). Two pointed aciculae per parapodium, protruding from parapodial lobes (Figs 12H, I, J). Ventral chaetae not seen. Pygidium conical, with two articulated and long anal cirri, with 14-15 articles, and one small medial papilla (Fig. 12C). Pharynx very long, through eight segments, with a conical, anterior tooth (Figs 12A, B). Proventricle long, through seven segments, 30 muscular cell-

rows (Fig. 12A).

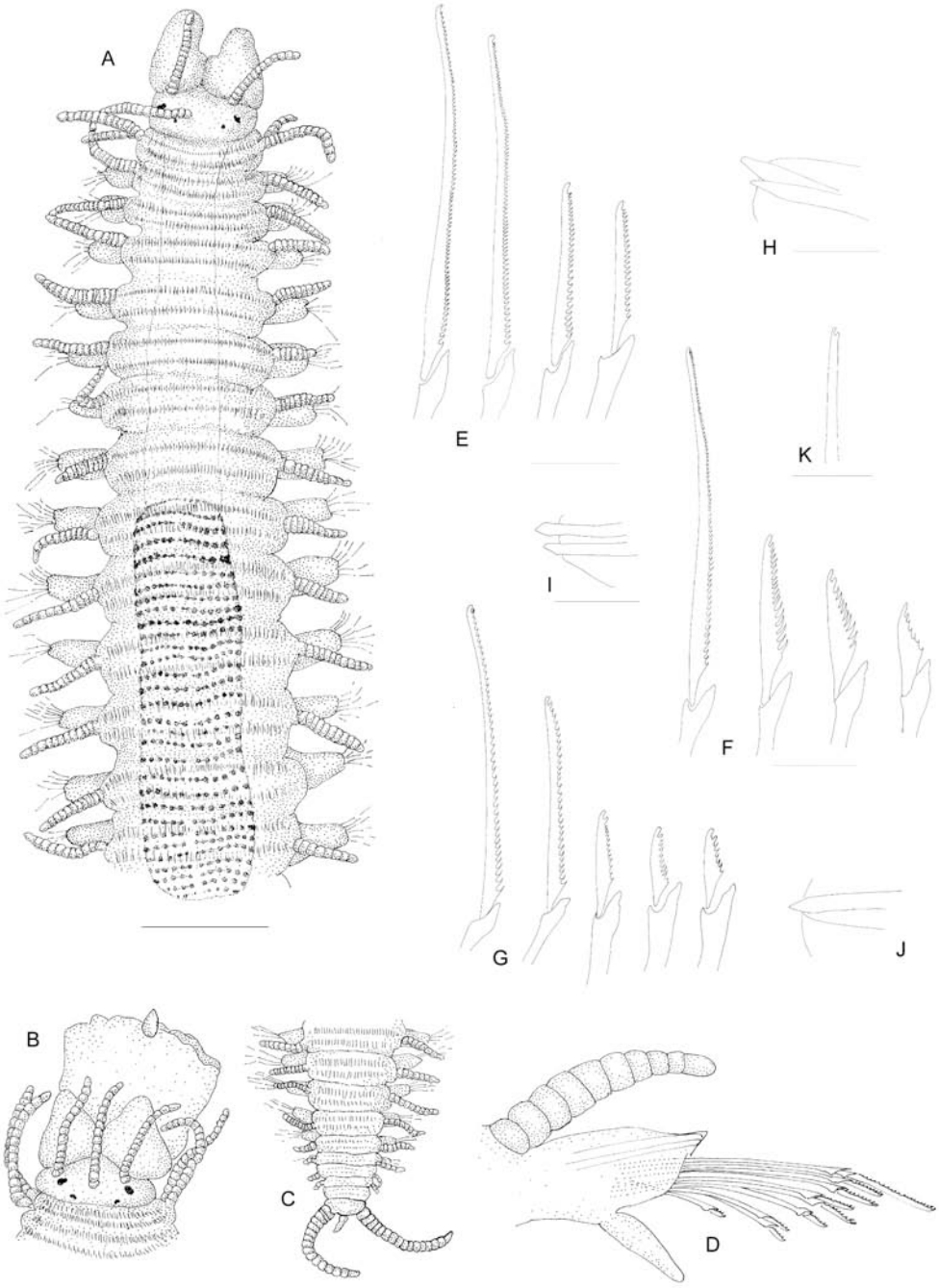

Figure 12. *Syllis pilosa* n. sp.: A, Anterior end, dorsal view, holotype MNCN 16.01/10141; B, Anterior end, dorsal view, paratype MNCN 16.01/10142; C, Posterior end, dorsal view, paratype MNCN 16.01/10142; D, Parapodium, posterior view, midbody chaetiger, holotype; E, Anterior chaetae, holotype; F, Midbody chaetae, holotype; G, Posterior chaetae, holotype; H, Anterior aciculae, holotype; I, Midbody aciculae, holotype; J, Posterior aciculae,, holotype; K, Dorsal simple chaeta, posterior chaetiger, holotype. Scale A-C: 0.4 mm; D: 0.2 mm; E-K: 20 µm.

Remarks

This species is mainly characterized by the presence of two marked ciliated bands per segment, elongated compound chaetae clearly bidentate on posterior segments and a long pharynx and proventricle. No species of the genus shows this combination of characters; only *Syllis barbata* San Martín, 1992, from Cuba, has been described having ciliated bands, but it lacks pseudospiniger chaetae and has a distinctive colour pattern (San Martín, 1992). Usually, members of the Syllinae lack ciliated bands, which are commonly found in members of the Eusyllinae (San Martín, 2003). Other species of the genus *Syllis* without ciliated bands, but with other similarities are: *Syllis beneliahuae* (Campoy and Alquézar, 1982), reported from the Mediterranean Sea, Atlantic and Pacific Ocean; *Syllis cornuta* (Rathke, 1843), reported from the northwest Atlantic, northwest Pacific, and other questionable localities (Licher, 1999); *Syllis parateinopterona* (Hartman and Fauchald, 1971) from the west Atlantic; and *Syllis aciculigrossa* (San Martín, 1990), from the Gulf of México. *Syllis beneliahuae* has compound pseudospiniger chaetae shorter in anterior chaetigers, and becoming longer towards (Campoy and Alquézar, 1982; Licher, 1999; San Martín, 2003), the opposite condition occurs in *S. pilosa* n. sp. Besides, aciculae are distally thicker and pointed in *S. beneliahuae*, but acuminate in *S. pilosa* n. sp. *Syllis cornuta* has similar compound chaetae, but the cirri are considerably longer and the dorsal simple chaeta is different (Licher, 1999). *Syllis parateinopterona* differs in having unidentate compound chaetae in posterior chaetigers and it lacks eyes (Hartman and Fauchald, 1971; Licher, 1999). Finally, the species *S. aciculigrossa* has very similar compound chaetae, principally the long and bidentate posterior pseudospinigers (San Martín, 1990), but it has only one thick acicula protruding from the parapodia.

Distribution. North West Pacific Ocean (Japan).

Etymology. The name comes from the Latin word "*pilus*" (=hair) and refers to the ciliated bands present on the dorsum.

Syllis rubicunda n. sp.

Figs 13, 14

Material examined. Holotype MNCN 16.01/10994 and paratypes MNCN 16.01/10995-10996 (2 specs). Shiraiso Coast, Manazuru, Sagami Bay, 35°09'14''N 139°08'49''E, intertidal to subtidal rocky shore, sea grass and algae, coll. by E. Nishi, September 2004, fixed and preserved in 95% ethanol. MNCN 16.01/11002-11003 (2 specs) Shiraiso Coast, Manazuru, Sagami Bay, 35°09'14''N 139°08'49''E, intertidal to subtidal rocky shore, sea grass and algae, coll. by E. Nishi, September 2004, fixed and preserved in 95% ethanol.

Comparative Material examined. *Syllis hawaiiensis* (Hartmann-Schröder, 1965) paratypes ZMH P-14495. U.S.A. Hawaii, Hilo, 20 April, 1959.

Syllis busseltonensis (Hartmann-Schröder, 1982) paratypes ZMH P-16761. Western Australia, Cape Naturaliste, Eagle Bay, eulitoral, algae and sand, 7 Nov, 1975.

Description

Holotype is a mature specimen, 5.5 mm long, and 0.6 mm wide with 56 chaetigers. Longer paratypes 5 mm long and 0.5 mm wide, with 53 chaetigers and 4 mm long, 0.5 mm wide, with 39 chaetigers, respectively. Body broad, thick and cylindrical, strongly pigmented orange-red. Pigmentation concentrated principally in posterior half of each segment and in two red, thin transversal lines on intersegmental groove (Fig. 13A). Prostomium wider than long, partially covered by peristomium, with two pairs of distinct red eyes in trapezoidal arrangement. Median antenna arising from middle of prostomium, slightly longer than combined length of prostomium and palps, with 30 broad articles; lateral antennae similar in shape and length to median one, inserted on anterior margin of prostomium, with about 28 articles. Palps broad and triangular, slightly longer than prostomium. Peristomium shorter than subsequent segments, with two pairs of tentacular cirri. Dorsal tentacular cirri with 40-45 broad articles, ventral ones with 30 articles (Fig. 13A). Dorsal cirri long, broad, longer than body width (Fig. 14A), alternating in length longer ones with about 40-60 articles, and shorter ones 20-30 (Fig. 13A). Internal spiral glands on edge of each article; organized in two rows along dorsal cirri (Fig. 13A). Posterior dorsal cirri longer than those of anterior region with about 65 articles. Ventral cirri short, not extending beyond parapodial lobes, conical in shape. Anterior parapodia each with about 12 compound, heterogomph chaetae, distal part of shafts provided

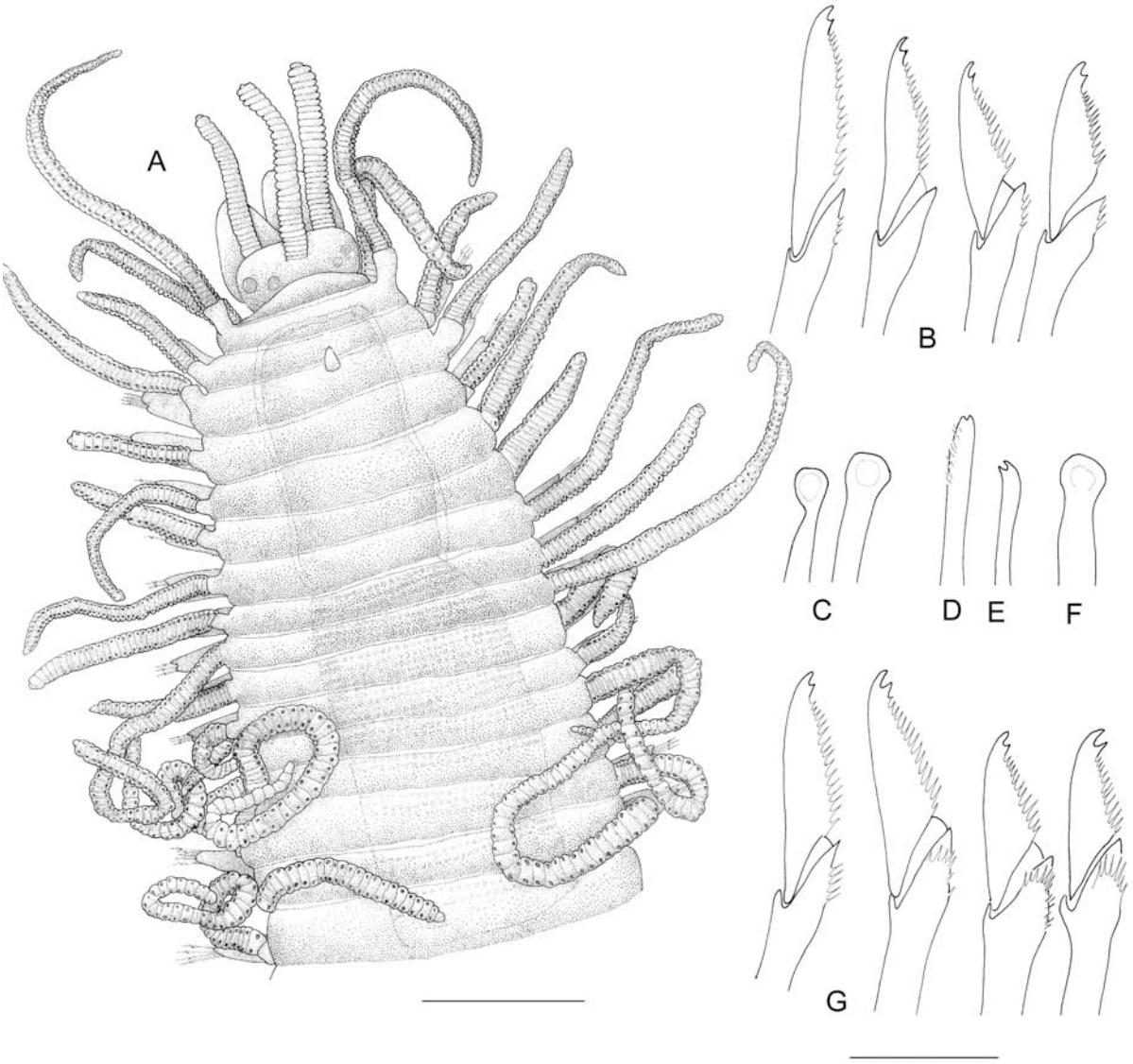

Figure 13. *Syllis rubicunda* n. sp. Holotype MNCN 16.01/10994: A, Anterior part, dorsal view; B, Anterior chaetae; C, Anterior aciculae; D, Dorsal simple chaeta, posterior parapodia; E, Ventral simple chaeta, posterior parapodia; F, Posterior acicula; G, Posterior chaetae. Scale A: 0.4 mm; B-G: 20 µm.

with spines and bidentate blades decreasing in length from dorsal (34.5 µm) to ventral (20 µm), with long spines on margin. Distal tooth slightly longer and wider than proximal one (Figs 13B; 14C). Midbody chaetigers with eight chaetae and posterior chaetigers with four to five chaetae, both similar in shape to anterior ones but slightly shorter (Figs 13G; 14D-H).

Midbody to posterior chaetigers with dorsal and ventral simple chaetae. Dorsal simple chaeta distally bifid with short subdistal spines on margin (Fig. 13D) and ventral simple chaetae distally bifid, smooth on margin (Fig. 13E). Two rounded and distally hollow aciculae per parapodia in midbody chaetigers and one in posterior segments (Figs 13C, F). Pygidium conical, with two long articulated anal cirri, longer than pygidium, with 30-35 articles (Fig. 14B). Pharynx extending through seven segments; conical tooth slightly back from anterior margin. Proventricle long and broad, extending through nine segments, cell-rows not visible (Fig. 13A).

Remarks

Syllis rubicunda n. sp. is characterised by its distinct colour pattern, broad and cylindrical body, long and thick dorsal cirri and bidentate chaetae. *Syllis rubicunda* is closely related to *Syllis prolifera* Krohn, 1852, from the Atlantic Ocean and Mediterranean Sea. Both species have the same kind of aciculae, distally rounded and hollow, and similar chaetae. However, *S. prolifera* lacks pigmentation or simply has fine black transversal bands on some anterior segments, and *S. rubicunda* n. sp. is distinctly pigmented orange, red and pink. Besides, dorsal cirri of *S. rubicunda* n. sp. are proportionally thicker than those of *S. prolifera*. Other similar species, with the pharyngeal tooth similarily located and the same kind of aciculae are: *Syllis vivipara* Krohn, 1859, also from the Mediterranean and Atlantic Ocean; *S. microoculata* (Hartmann-Schröder, 1965), from Hawaii; *S. busseltonensis* Hartmann-Schröder, 1982, from Western Australia and Polynesia; and *S. hawaiiensis* (Hartmann-Schröder, 1965) from Hawaii. However, none of these species have a similar colour pattern. In addition, *S. vivipara* has compound chaetae with unidentate or undistinctly bidentate blades (San Martín, 2003); *Syllis microoculata* has papillae on both sides of the body (Hartmann-Schröder, 1965); *S. busseltonensis* has slender chaetae with shorter spines and shorter proventricle; and the dorsal cirri and proventricle of *S. hawaiiensis* are shorter.

Distribution. North West Pacific Ocean (Japan).

Etymology. The specific name derives from '*rubicunda*= red' in Latin and refers to the colour pattern.

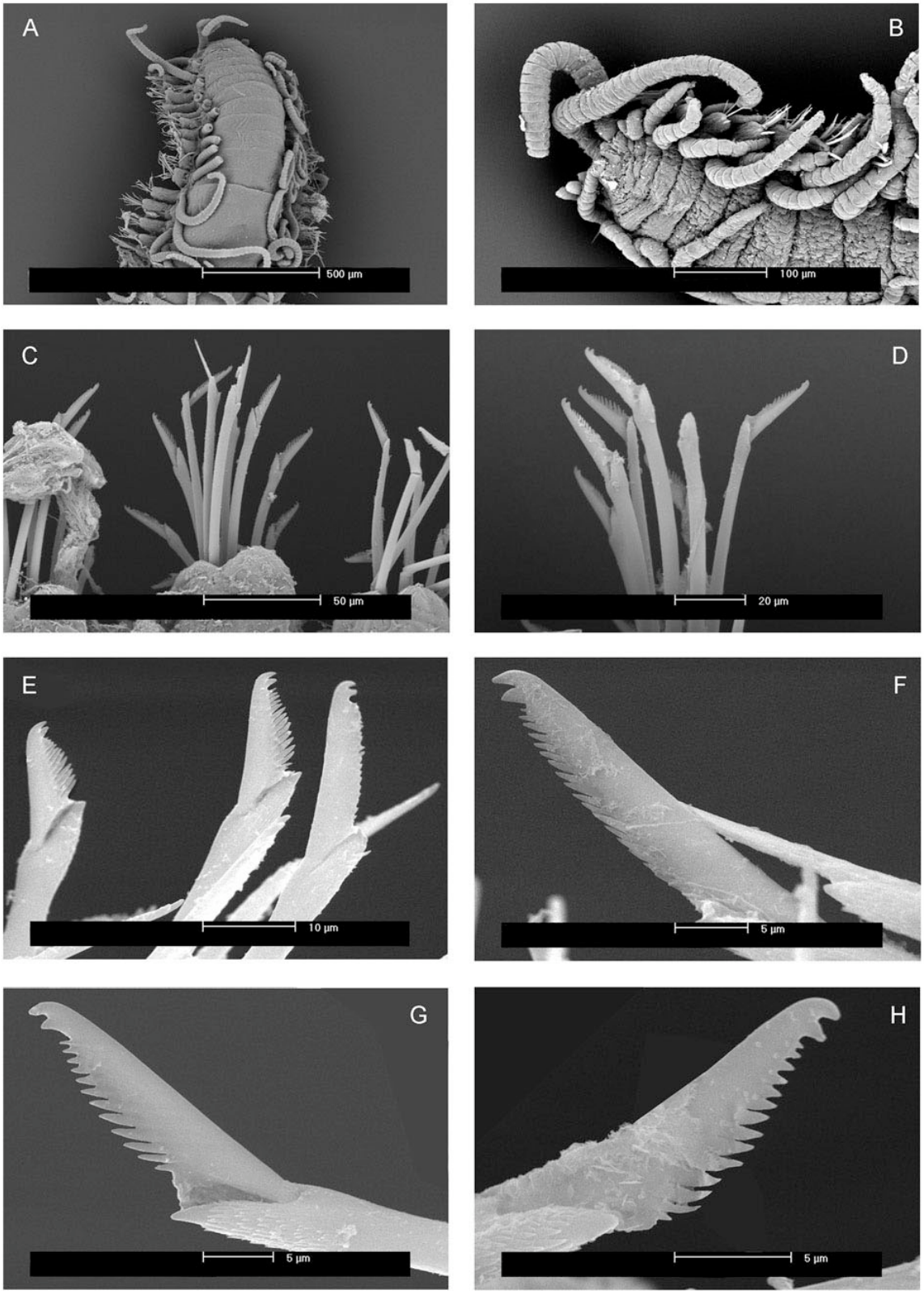

Figure 14. *Syllis rubicunda* n. sp. SEM. MNCN 16.01/11002: A, Anterior part, dorsal view; B, Posterior part, dorsal view; C, Anterior chaetae; D -H, Midbody chaetae.

Genus *Trypanoseta* Imajima and Hartman, 1964 (emended)

Trypanosyllis (Trypanoseta) Imajima and Hartman, 1964: 129.

Geminosyllis Imajima, 1966d: 233. Kudenov and Harris, 1995: 71, fig. 1.26.

Type species. *Trypanosyllis (Trypanoseta) ohma* (Imajima and Hartman, 1964).

Diagnosis.

Body subcylindrical, segments moderately long. Prostomium pentagonal with two pairs of eyes. Median antenna arising between posterior pair. Palps large, broadly triangular, free at bases. Pharynx with a trepan with ten teeth and a large, middorsal tooth; ten soft papillae at margin. Antennae, tentacular, dorsal and anal cirri articulated, conical and whip-shaped. Simple chaetae subdistally thickend and distally bifid, three to seven per parapodium. Simple capillary chaetae on posterior parapodia.

Remarks

Imajima (1966d) considered that *Trypanosyllis (Trypanoseta) ohma* described by Imajima and Hartman (1964) represented a new genus, which he named *Geminosyllis*. However, following the Principle of Priority, articles 23.1 (Statement of the Principle of Priority) and 23.3 (Application to synonymy) of the International Code of Zoological Nomenclature (4th edition, 2000), this genus should have been named *Trypanoseta*. The name of the subgenus becomes the new generic denomination and *Geminosyllis* becomes superfluous.

Trypanoseta ohma (Imajima and Hartman, 1964) n. comb.

Figs 15, 16

Trypanosyllis (Trypanoseta) ohma Imajima and Hartman, 1964: 129-130, fig. 31.

Geminosyllis ohma Imajima, 1966d: 233-235, fig. 43. Kudenov and Harris, 1995: 71-72, fig. 1.26.

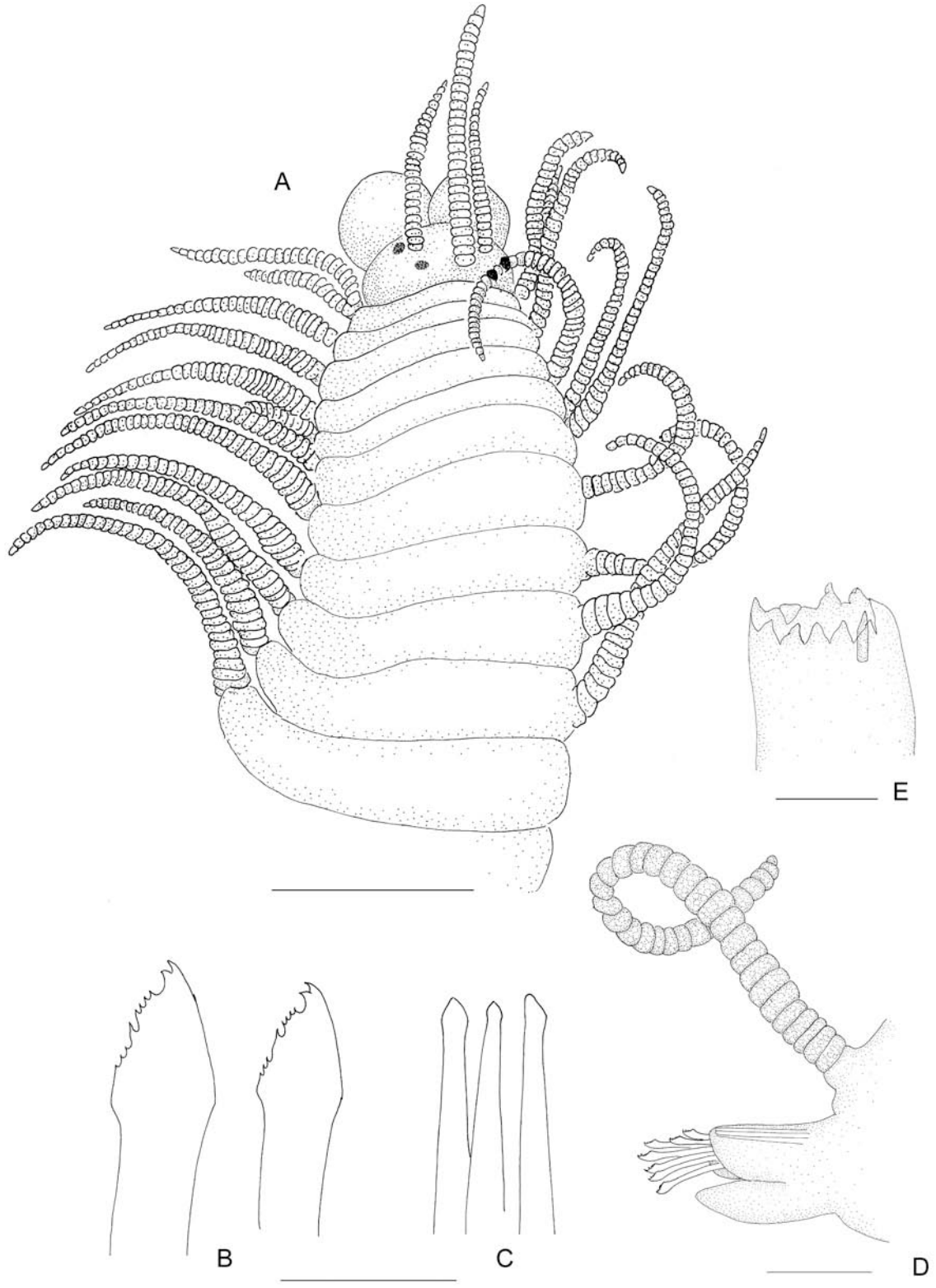

Figure 15. *Trypanoseta ohma* n. comb. CBM-ZW 997: A, Anterior part, dorsal view; B, Midbody chaetae; C, Aciculae; D, Midbody parapodium, anterior view; E, Anterior end of the pharynx. Scale A: 0.5 mm; B, C: 20 µm; D: 0.2 mm; E: 0.4 mm.

Material examined. CBM-ZW 996 (1 spec.) Tokyo Bay to Uraga Channel, 35°09’18’’N 139°47’51’’E, 79 m, rocky shore, November 1995.

Description

Incomplete specimen 13 mm long, 1 mm wide, with about 67 segments. Body dorsally arched and ventrally flattened, yellow to orange. Prostomium wider than long, with two pairs of eyes in trapezoidal arrangement, anterior ones slightly larger than posterior (Fig. 15A). Median antenna inserted on middle of prostomium, longer than combined length of prostomium and palps, with 30 articles; shorter lateral antennae inserted on anterior margin of prostomium, with 25 articles. Palps triangular to rounded, longer than prostomium, free at bases. Peristomium shorter than subsequent segments, with two pairs of tentacular cirri. Dorsal tentacular cirri similar in length to lateral antennae, with 25 articles, ventral ones shorter, with 17 articles (Fig. 15A). Dorsal cirri of anterior and midbody segments slightly alternating in length, longer cirri with 35 articles, shorter with 30. All dorsal cirri conical and whip-shaped, with wide, basal articles becoming shorter and with narrower tips, and granular material inside articles (Fig. 15A). Cirrophores present. Ventral cirri digitiform, inserted proximally on parapodia, slightly extending beyond parapodial lobes. Pre- and postchaetal lobes present, both similar in length (Fig. 15D). Chaetal fascicles with five to seven simple chaetae, two most dorsally located shorter and smaller (Figs 15D; 16A). All blades bidentate with both teeth similar in length and short spines on edge distributed in two groups, one group more distally with four to five spines, second group with three to four small spines, arising from lower level and one thicker spine between both groups (Figs 15B; 16B-D). Three straight aciculae per parapodia, slightly distally enlarged (Fig. 15C). Pygidium lacking. Pharynx reddish to brown, extending through 13 segments; conical tooth on anterior margin. Long proventricle extending through 14 segments, 50 cell-rows. Pharynx border with ten soft papillae. Edge of the pharynx with ten soft triangular projections (Fig. 15E).

Remarks

The presence of a trepan was considered a diagnostic character of the genus by Imajima (1966d) and is an important difference from other genera with similar chaetae, such as *Haplosyllis*. However, the specimen studied does not have a real trepan, the terminal projections located on anterior margin of the pharynx are not chitinous and some of them are

curving. In contrast, some specimens of *Haplosyllis* are known to have a chitinous edge of the pharynx that could be confused with teeth (San Martín, 2003). The presence of a trepan in this genus is thus probably a more plastic character than has been considered, and is possibly not a clear diagnostic character.

Distribution. North Pacific Ocean (Kurile Islands, Russia, Southern California, Japan).

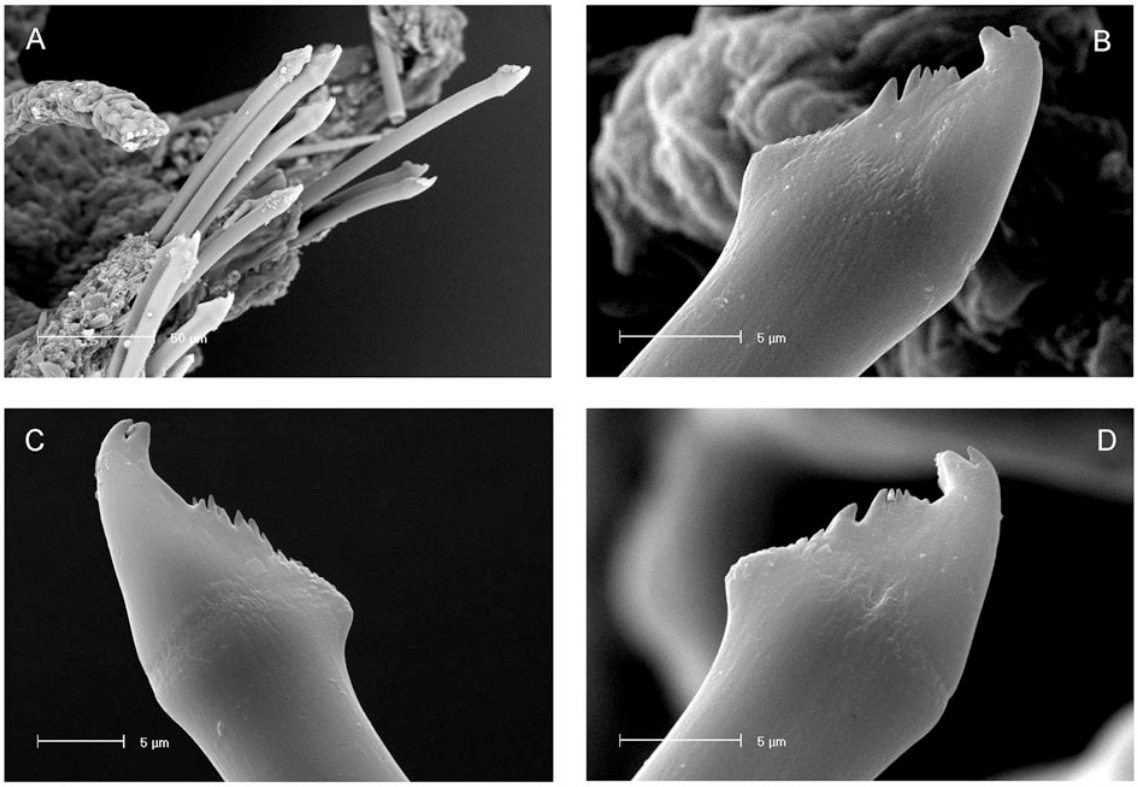

Figure 16. *Trypanoseta ohma* n. comb. SEM. CBM-ZW 997: A, Midbody chaetae; B, Anterior chaeta; C, Midbody chaeta; D, Posterior chaeta.

Trypanosyllis zebra (Grube, 1860)

Syllis zebra Grube, 1860: 86.

Trypanosyllis (Trypanosyllis) zebra Imajima, 1966d: 236

Trypanosyllis zebra Licher, 1999: 295, 296. San Martín, 2003: 311-315, figs 171-173.

Material examined. CBM-ZW 997 (1 spec.) Shiraiso Coast, Manazuru, Sagami Bay, 35°09’14’’N 139°08’49’’E, intertidal to subtidal rocky shore, sea grass and algae, coll. by E. Nishi, September 2004.

Distribution. Apparently cosmopolitan.

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A new species of *Opisthosyllis* (Polychaeta: Syllidae) from California (U.S.A.)

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Abstract

Opisthosyllis leslieharrisae n. sp. is described from Santa Catalina Island, California. It differs from all other species of the genus in the following characters: dorsum densely covered by papillae in two sizes, and a distinct colour pattern consisting of white spots distributed transversally along the segments (only seen in live specimens) and dark red areas located on cirrophores, over the third segment, and in the middle of the second and the remainder segments (maintained in formalin fixed specimens). The new species is also characterized by the tooth located in the third quarter of the pharynx, and long spines on the blades of compound chaetae.

Key Words: *Opisthosyllis*, Syllidae, polychaetes, taxonomy, new species.

Introduction

The genus *Opisthosyllis* was established by Langerhans (1879) when he described *O. brunnea*, the type species of the genus, and *O. viridis* from the Madeira Island in the Atlantic Ocean. *Opisthosyllis* was diagnosed by a combination of characters, with one of them being used for the etymology; the presence and location of the pharyngeal tooth in the posterior part of the pharynx. Other features used to diagnose the genus were an elongated body with numerous segments, palps fused at the base, a prostomium with three antennae, tentacles and dorsal cirri jointed, and a conical ventral cirri. Later on, in the beginning of the twentieth century, several authors (Verrill 1900; Augener 1913; Fauvel 1921; Monro 1939) added new species to the genus extending its distribution to other localities in the Atlantic Ocean (*Opisthosyllis nuchalis* Verrill, 1900 from Bermudas), as well as the Indian Ocean (*Opisthosyllis australis* Augener, 1913 from Western Australia, and *Opisthosyllis ankylochaeta* Fauvel, 1921 from Madagascar), and the Red Sea

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(*Opisthosyllis longocirrata* Monro, 1939). During the 1950s and 1960s, Day (1957), Hartmann-Schröder (1959, 1960, 1965), and Imajima (1966) continued discovering new species including *Opisthosyllis laevis* Day, 1957 from Mozambique, *Opisthosyllis arboricola* Hartmann-Schröder, 1959 from El Salvador, *Opisthosyllis papillosa* Hartmann-Schröder, 1960 from the Red Sea, *Opisthosyllis corallicola* Hartmann-Schröder, 1965 from Hawaii, and *Opisthosyllis japonica* Imajima, 1966 from Japan. The most recent additions to *Opisthosyllis* are the works of Hartmann-Schröder (1981), San Martín (1991), and Lee & Rho (1994). Those are *Opisthosyllis simpliseta* Hartmann-Schröder, 1981 from the Western Australia, *Opisthosyllis longidentata* San Martín, 1991 from Florida, and *Opisthosyllis convexa* Lee & Rho, 1994 from Korea.

Two other taxa have been allocated to *Opisthosyllis* that we do not consider being part of the genus, namely *Opisthosyllis brevicirra* Hartmann-Schröder, 1979, and *Opisthosyllis dorsoaciculata* Hartmann-Schröder, 1991. The former taxon has been re-allocated by the same author to a different genus *Paraopisthosyllis* Hartmann-Schröder, 1991, differing from *Opisthosyllis* in having smooth and clubshaped dorsal cirri. The latter taxon most likely does not belong within *Opisthosyllis* as it has, for instance, the pharyngeal tooth on the anterior part of its pharynx and tetra lobed palpi.

There are several diagnoses of the genus *Opisthosyllis* given by different authors (Imajima 1966; Day 1967; San Martín 1984; San Martín 2003; Capa 2004). The diagnosis followed in this paper is that of San Martín (2003): Body with numerous segments, three antennae, two pairs of eyes, palps partially fused at base, two pairs of tentacular cirri, some species with an occipital flap; long dorsal cirri; antennae, tentacular cirri and dorsal cirri articulated; pharynx with papillae and one tooth located in its posterior part, sometimes at the end of the pharynx; parapodia with compound chaetae, simple dorsal and ventral chaetae in some segments, and reproduction by schizogamy.

In this paper we describe *Opisthosyllis leslieharrisae* n. sp. from California (Santa Catalina Island). We compare this new species, with all other 14 *Opisthosyllis* species hitherto described in Table 1. *Opisthosyllis leslieharrisae* appears to be most similar to other *Opisthosyllis* taxa with the dorsum covered by papillae, including *O. viridis*, *O. papillosa* and *O. convexa*.

Material and methods

The material was collected on Santa Catalina Island, California in January, 2001. The specimens were fixed in a 10% formaldehyde-seawater solution and preserved in a 70% alcohol solution. Additional material was fixed in 80% alcohol for DNA analysis. For identification, an Olympus SZ30 stereomicroscope and Olympus CH30 optic microscope were used. Drawings were made to scale, with a camera lucida drawing tube in a Nikon Optiphotoptic microscope equipped with interference contrast optics (Nomarsky). Pictures from scanning electron microscopy (SEM) were taken at the SIDI (Servicio

Interdepartamental de Investigación), Universidad Autónoma de Madrid (UAM). Photographs were taken with a Nikon F50 camera attached via a phototube to a compound microscope. Width of the specimens is measured at level of proventricle, excluding parapodia. Holotype and paratypes from *Opisthosyllis leslieharrisae* n. sp. are deposited at the Museo Nacional de Ciencias Naturales (MNCN) in Madrid, Spain. Comparative material examined of other *Opisthosyllis* species were loaned by the Hamburgische Zoologische Museum (HZM) and the Universidad Autónoma de Madrid (UAM).

Taxon Description

Family SYLLIDAE Grube, 1850
Genus *Opisthosyllis* Langerhans, 1879
***Opisthosyllis leslieharrisae* sp. nov.**
(Figures 1–4)

Material examined. USA: holotype [MNCN 16.01/10264], 3 paratypes [MNCN 16.01/10265 (1), MNCN 16.01/10266 (2)], 3 spms., Santa Catalina Island, Wrighley Marine Science center: 33°26.7 N, 118°29.1W; 1–4 m, *Corallina*, *Sargussum*, red algae, hydroids, bryozoans and sponges, 15 Jan. 2001. Coll. A. Nygren, J. Toth.

Comparative material examined.

Opisthosyllis papillata Hartmann-Schröder, 1960. Paratype [P-14718-HZM].

Opisthosyllis viridis Langerhans, 1879. Several specimens. Cabo Verde Islands [Polychaetes collection, UAM].

Opisthosyllis australis Augener, 1913. Type material [V7947-HZM].

Diagnosis. *Opisthosyllis* with dorsum densely covered by papillae in two sizes, tooth located in the third quarter of the pharynx, long spines on blades of compound chaetae, and a distinct colour pattern consisting of white spots (live specimens) and dark red areas distributed over dorsum (maintained in preserved specimens).

Description.The holotype is 7.6 mm long, 0.48 mm wide, with 73 chaetigers, adult specimen. Paratypes are 9.5 mm long, 0.7 mm wide, 54 chaetigers (MNCN16.01/10265); 6.4 mm long, 0.5 mm wide, 32 chaetigers and 2.1 mm long, 0.5 mm wide, 30 chaetigers (anterior fragment) (MNCN 16.01/10266). Body shape, excluding parapodia, circular in section, venter flattened; body width fairly constant with tapering end. Body in outline long and slender, posteriorly broken, with signs of regeneration in all specimens (Fig. 1B, E). Live specimens with distinct colour pattern (Figs. 1A–E): white area in chaetigers 1 and 2; chaetiger 3 dorsally pigmented in red, following segments with a reddish oval area at midline of body; tentacular cirri and dorsal cirri of all segments with an oval to circular area of reddish pigment on and around the cirrophores. Colour markings more distinct on the cirri pointing up than on cirri pointing down. White spots in transversal rows on each segment, and white fibrilar material in cirral articles. The red colour pattern is preserved in

formalin fixed specimens (Fig. 2A). Dorsal surface covered with triangular papillae in two sizes (Fig. 3E, F), more distinct posteriorly to proventricle (Figs. 1E, 2A). Prostomium wider than long, rectangular to oval, with two pairs of red eyes with lenses, in trapezoidal arrangement, anterior pair larger (Fig. 1A); eye spots absent. Palps broad, fused at base, with visible, central groove; palps slightly longer than prostomium. Median antenna inserted medially on prostomium, longer than prostomium and palps together, with 23 articles. Lateral antennae inserted on anterior margin of prostomium (Figs. 2A, 3B) with 14–15 articles, approximately half the length of median antenna. Ceratophores present (Fig. 3C). Two ciliated areas present between base of median antenna and bases of both lateral antennae (Fig. 3C). Two ciliated nuchal organs present lateral and behind the prostomium (Fig. 3B, C). Peristomium shorter than subsequent segments, anterior margin of peristomium ciliated and prolonged, partially covering the prostomium (Fig. 3C). Dorsal tentacular cirri with 33 articles, ventral pair shorter, with 25 articles. Dorsal cirri of chaetiger one shorter than tentacular cirri, with 22 articles, second dorsal cirri similar in length to first dorsal cirri, with 20 articles, third and fourth dorsal cirri longer, with 34 and 32 articles (Figs. 1C, 2A, 3B). Subsequent cirri alternating in length with 20–35 articles, longer ones pointing up and shorter ones pointing down (Fig. 1C, E). Alternation in direction of cirri starting from chaetiger 1, where D=cirri pointing down and U=cirri pointing up, with the following formula UDDUDUDDU followed by DU-groups to the posterior end. Distinct alternation in median chaetigers (Fig. 1D). Cirrophores well developed. Antennae, tentacular and dorsal cirri with minute ciliation on articles (Fig. 3G). Ventral cirri oval and short, proximally inserted and not extending beyond tips of parapodia (Fig. 3D). Pre- and postchaetal as well as dorsal lobes, all similar in length, present on all parapodia (Fig. 3H). Chaetal fascicle with 10–12 heterogomph compounds in anterior chaetigers, 3–6 in median and posterior; distal part of shafts provided with spines. Compound chaetae with bidentate blades, distal tooth longer and broader than proximal one, blade edge with long spines, blades dorsoventrally gradiated in length (Figs. 2B, G, 3I, 4A–D). Length of dorsalmost chaetal blades c. 35 µm in anterior parapodia (Fig. 2B), and c. 28 µm in median parapodia (Fig. 2G). Dorsal and ventral simple chaetae distally bifid (indistinct in ventral ones) with short subdistal spines on margin (Figs. 2E, 4E). Ventral simple chaetae only observed in last segment of holotype (Figs. 2F, 4F). Three aciculae in anterior parapodia (Fig. 2C), one in median and posterior (Fig. 2D), all distally blunt. Pygidium regenerating, no anal cirri, median papilla absent. Paratype MNCN 16.01/ 10265 with two anal cirri, pygidium also regenerating (Fig. 1B). Pharynx shorter than proventricle, almost as broad as proventricle; large conical tooth located in the third quarter of the pharynx (Fig. 1A, 2A). Proventricle shape cylindrical, through segment 10 to 18, with 40–50 cell-rows (Fig. 1D, 2A).

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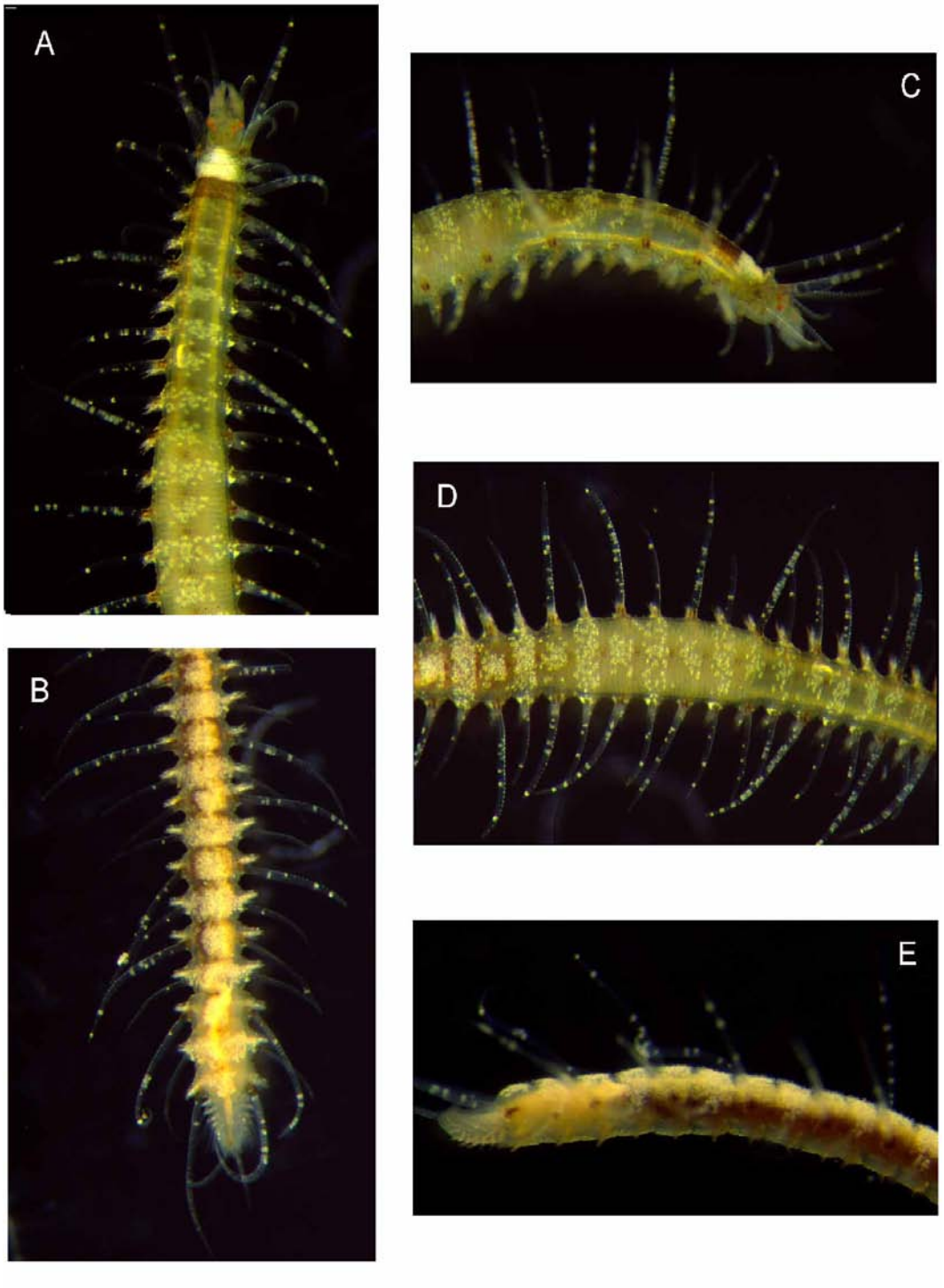

FIGURE 1. *Opisthosyllis leslieharrisae* n. sp. Paratype MNCN 16.01/10265. Live specimen. A: Anterior end, dorsal view; B: Posterior end, dorsal view; C: Anterior end, lateral view; D: Proventricle level, dorsal view; E: Posterior end, lateral view.

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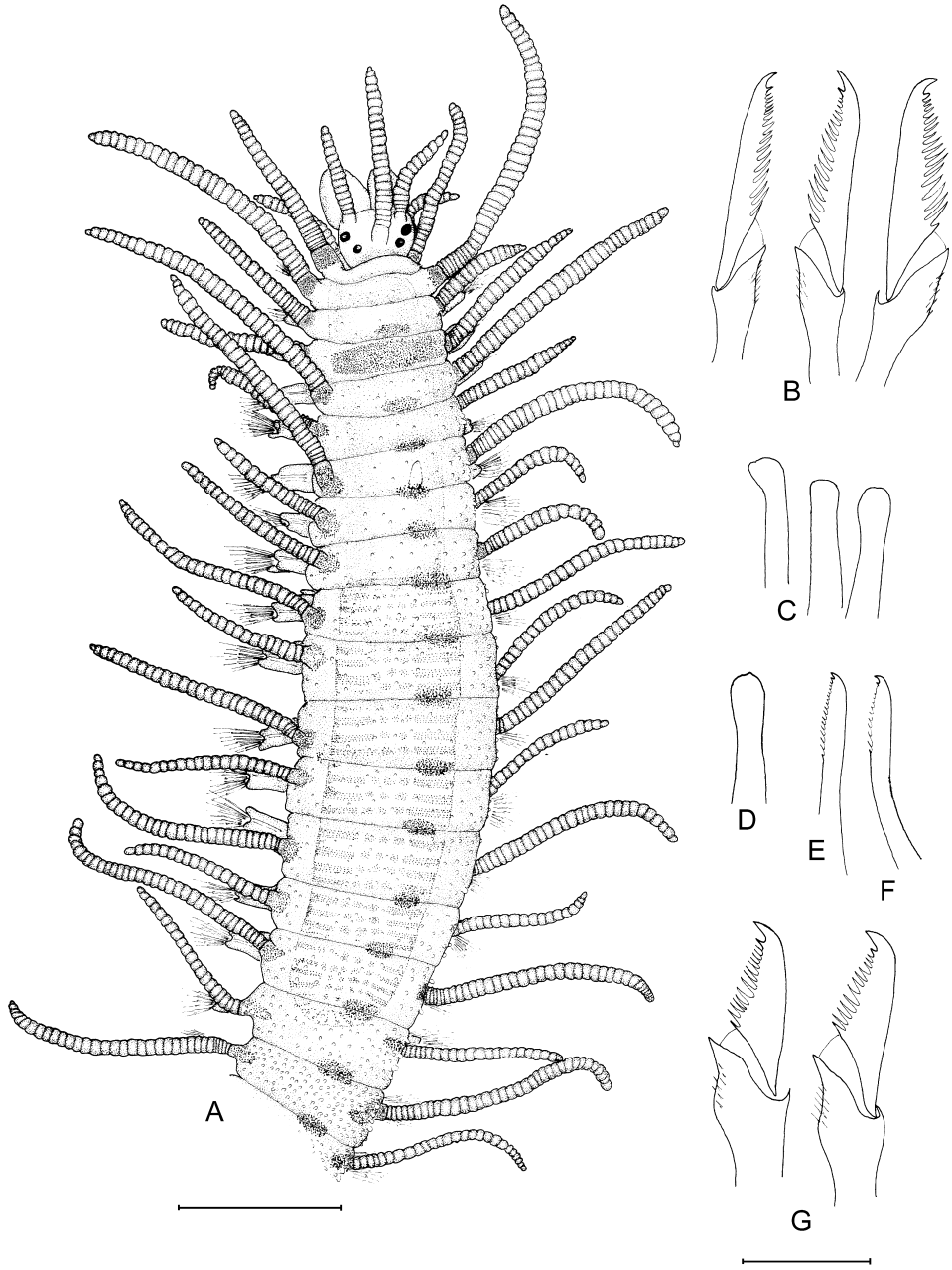

FIGURE 2. *Opisthosyllis leslieharrisae* n. sp. Holotype MNCN 16.01/10264, drawn from preserved specimen. A: dorsal view; B: Compound chaetae, anterior chaetiger; C. Aciculae, anterior chaetiger; D: Acicula, median chaetiger; E: Dorsal simple chaetae, median chaetiger; F: Ventral simple chaetae, last chaetiger, G: Compound chaetae, median chaetiger. Scale A 0.4 mm; D–G: 20 μm.

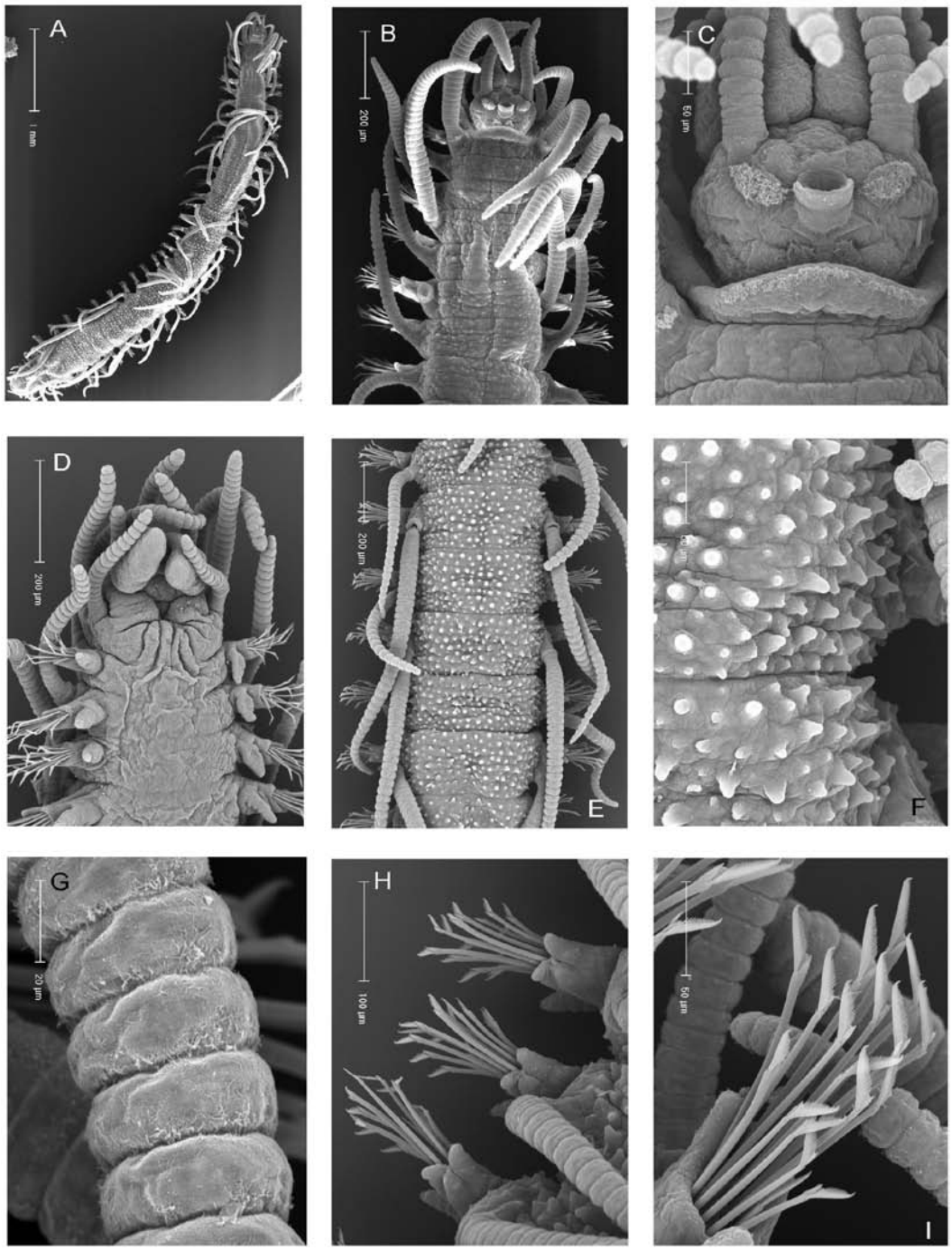

FIGURE 3. Scanning electron micrographs (SEM). *Opisthosyllis leslieharrisae* n. sp. Paratype MNCN 16.01/10266. A: Dorsal view; B: Anterior part, dorsal view; C: Prostomium and peristomium, dorsal view; D: Anterior part, ventral view; E: Dorsum of median chaetigers; F: Papillae in two different sizes over dorsum; G: Ciliated cirri articles; H: Median parapodia, dorsal view; I: Anterior parapodia, ventral view.

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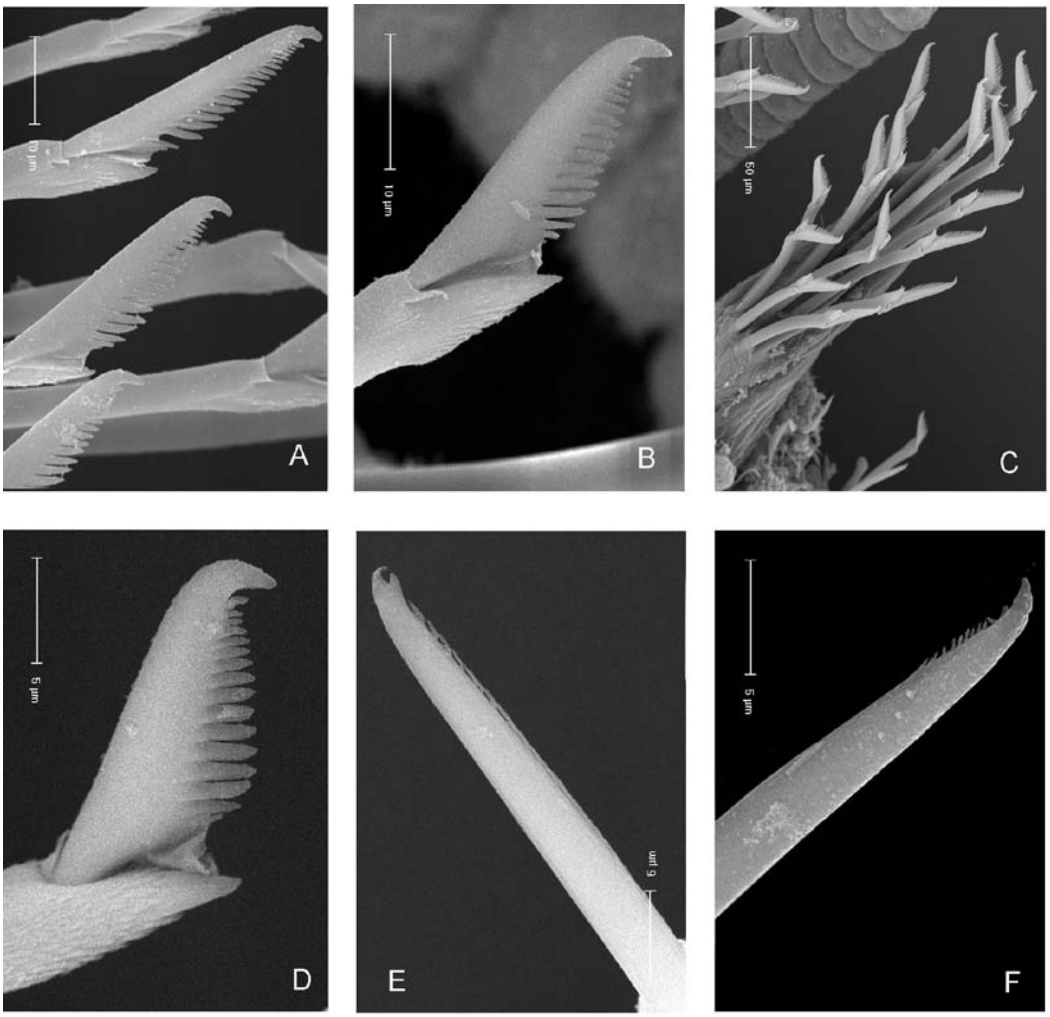

FIGURE 4. Scanning electron micrographs (SEM). *Opisthosyllis leslieharrisae* n. sp. Paratype. MNCN 16.01/10266. A, B: Compound chaetae, anterior chaetiger; C: Median parapodia, ventral view; D: Compound chaetae, median chaetiger; E: Dorsal simple chaeta; F: Ventral simple chaeta.

Remarks

Opisthosyllis leslieharrisae n. sp. is characterized by the position of the tooth in the third quarter of the pharynx, a dorsum densely covered by papillae in two sizes, long spines on blades of compound chaetae, and a distinct colour pattern.

There are only three other species in *Opisthosyllis* with a papillated dorsum, namely *O. viridis*, *O. papillosa*, and *O. convexa*. *Opisthosyllis australis*, although described with papillae, only presents some rugosities in the lateral part of parapodia as an artefact from the fixation (Capa pers. com.).

These four papillated species also share the presence of cirri alternating in length; however, these are usually considerably shorter in *O. viridis, O. papillosa* and in *O. convexa. Opisthosyllis viridis* has 8–12 articles (Langerhans 1879; Núñez et al. 1992), *O. papillosa* 14–20 articles (Hartmann-Schröder 1960, 1965, 1991), and *O. convexa* 11–22 articles (Lee & Rho 1994) in their anterior parapodia, while *O. leslieharrisae* has 20–35 articles. *Opisthosyllis leslieharrisae* may further be separated from the other papillated taxa in having much longer spines on the edge of its compound chaetae, dorsal papillae that are triangularly shaped, and of two different sizes, compared with rounded and of the same size in *O. viridis*, *O. convexa* and *O. papillosa* (Capa 2004), and finally a pharyngeal tooth that is positioned in the third quarter of the pharynx, compared with the posteriormost part in the other papillated species. *Opisthosyllis leslieharrisae* shares the position of the tooth with *O. laevis* and *O longidentata,* but both of these taxa lack dorsal papillae and the colour pattern found in *O. lesliharrisae*. Principal differences between *O. leslieharrisae* and all other 14 species of the genus are summarized in Table 1.

TABLE 1. A list of selected characters for *Opisthosyllis leslieharrisae* sp. nov. and the other species of the genus.

Species	Tooth position	Papillae	Chaetae	Colour Pattern	Distribution (Type localities in bold)	References
O. leslieharrisae	Middle-posterior	Small, triangular, two sizes	Bidentate falcigers, long spinulation	White spots over segments (live specimens) and dark red areas on cirrophores, middle of segments and over the third segment (formalin fixed specimens).	Pacific Ocean (**California, USA**)	
O. laevis Day, 1957	Middle-posterior	Absent	Bidentate falcigers, short spinulation	Absent in preserved material	Indian Ocean (**Mozambique**, Madagascar)	Day 1957
O. convexa Lee & Rho, 1994	Posterior	Small, digitiform, one size	Bidentate falcigers, short spinulation	Body creamy coloured, without colour markings (formalin fixed specimens).	Pacific Ocean (**Korea**)	Lee & Rho 1994; Capa 2004
O. papillosa Hartmann-Schröder, 1960	Posterior	Small, digitiform, one size	Bidentate falcigers, short spinulation	Absent in preserved material	**Red Sea**, Pacific Ocean (Hawaii Islands), Indian Ocean (Australia)	Hartmann-Schröder 1960,1965, 1981, 1991; Capa 2004
O. viridis Langerhans, 1879	Posterior	Small, digitiform, one size	Bidentate falcigers, short spinulation	Absent in preserved material	Atlantic Ocean (**Madeira Island**, Canary Islands, Cabo Verde Islands), Pacific Ocean (Japan, Marquesas Islands)	Langerhans 1879; Monro 1939; Núñez *et al*. 1992; López & San Martín 1994; Lee & Rho 1994; Imajima 1966; Capa 2004

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TABLE 1 (continued)

Species	Tooth position	Papillae	Chaetae	Colour Pattern	Distribution (Type localities in bold)	References
O. nuchalis Verril, 1900	Posterior	Absent	Unidentate falcigers, short spinulation	Yellowish white (formalin fixed specimens)	Atlantic Ocean (**Bermudas**, Florida)	Verrill, 1900; Hartmann-Schröder 1959
O. australis Augener, 1913	Posterior	Absent	Bidentate falcigers, unidentate in posterior part, short spinulation	Yellowish white (formalin fixed specimens)	Indian Ocean (**Australia**, India, Ceylon), Pacific Ocean (Gambier Islands, New Caledonia)	Augener 1913; Hartmann-Schröder 1981, 1991
O. ankylochaeta Fauvel, 1921	Posterior	Absent	Unidentate falcigers and simple chaetae (blades fused to the shafts), short spinulation	Not described	Indian Ocean (**Madagascar**), Pacific Ocean (New Caledonia)	Fauvel 1921; Day 1967;
O. longocirrata Monro, 1939	Posterior	Absent	Bidentate falcigers, short spinulation	Absent in preserved material	**Red Sea**, Indian Ocean (Maldives Islands), Pacific Ocean (Tahiti Island)	Monro 1939; Hartmann-Schröder 1960
O. arboricola Hartmann-Schröder, 1959	Posterior	Absent	Unidentate falcigers, short spinulation	Not described	Pacific Ocean (**El Salvador)**	Hartmann-Schröder 1959
O. corallicola Hartmann-Schröder, 1965	Posterior	Absent	Bidentate falcigers, unidentate in posterior part, short spinulation	Not described	Pacific Ocean (**Hawaii Islands**)	Hartmann-Schröder 1965; Westheide 1974
O. japonica Imajima, 1966	Posterior	Absent	Bidentate falcigers, Unidentate in posterior part, two thick simple chaetae, short spinulation	Pale yellowish green (live specimens). Colour not preserved (formalin fixed specimens).	Pacific Ocean (**Japan**)	Imajima 1966
O. simpliseta Hartmann-Schröder,1981	Posterior	Absent	Bidentate falcigers and unidentate in posterior part, thick simple chaetae, short spinulation	Absent in preserved material	Indian ocean (**Australia)**	Hartmann-Schröder, 1981
O. longidentata San Martín, 1991	Middle-Posterior	Absent	Bidentate falcigers, long spinulation	Absent in preserved material	Atlantic Ocean (**Florida**)	San Martín 1991
O. brunnea Langerhans, 1879	Posterior	Absent	Unidentate falcigers, short spinulation	Yellowish white (formalin fixed specimens)	Atlantic Ocean (**Madeira Island** to South Africa)**,** Indian Ocean (Mozambique, Somalia, Australia), Pacific Ocean (Japan, Korea & Panama), Mediterranean Sea	Langerhans 1879; San Martín 1984; Imajima 1966; Day 1967; Hartmann-Schröder 1981, 1991; Lee & Rho 1994

Etymology

This species is dedicated to Leslie Harris (Natural History Museum of Los Angeles County) for her remarkable contributions to the knowledge of polychaetes, her unconditional support and efficiency loaning specimens to the authors, and not the least, her warm hospitality.

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We wish to express our gratitude to our college Dr. María Capa for fruitful discussions and sharing her knowledge on species of genus *Opisthosyllis*, and to Jenny Toth for help in collecting the specimens. We also thanks to Angelika Brandt and Gisella Wegener for (HZM) for loaned material and to Jesús Marugán for his style suggestions in final version of the manuscript.

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Syllidae (Annelida: Polychaeta) from Indonesia collected by the Siboga (1899-1900) and Snellius II (1984) expeditions

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Abstract

Twenty seven samples of syllids (Annelida: Polychaeta) from Indonesia collected during the Siboga Expedition (1899-1900) and five during the Snellius II Expedition (1984) have been examined. Material from several other Museums and Institutions has also been included. Unpublished identifications of Siboga material by Augener have been checked and all specimens have been named according to current taxonomic knowledge. A total of 30 taxa have been identified, belonging to 10 different genera: *Branchiosyllis*, *Haplosyllides*, *Eusyllis*, *Odontosyllis*, *Opisthosyllis*, *Paraehlersia*, *Pionosyllis*, *Sphaerosyllis*, *Syllis* and *Trypanosyllis*. Four species are described as new: *Opisthosyllis mariae*, *Syllis komodoensis*, *Syllis villenai* and *Syllis ypsiloides*. One previously synonymised species, *Syllis augeneri*, is re-described herein as valid. Two more taxa are proposed as new combinations, and four are reported as cf. either due to lack of enough representative specimens or to variability in diagnostic characters or geographical distribution. Finally, two taxa are described but unnamed because of paucity of material. All new species and reports for the area are described and figured.

Key words: Syllidae, Polychaetes, Taxonomy, new species, Indonesia.

Index

Introduction

The Dutch Siboga Expedition to the Indonesian archipelago was one of the historically most important oceanographic expeditions of the end of the Nineteenth century (Van Aken, 2005). Under the initiative of the Society for the Advancement of Scientific Research in the Dutch Colonies, the Siboga Expedition was organized to enable a series of zoological, botanical, oceanographical and geological explorations in deep Indonesian waters. The expedition was led by Dr. M. Weber, director of the Zoological Museum of Amsterdam and professor of the University of Amsterdam and took place in the Dutch East Indies (now Indonesia) during 1899 and 1900. The principal aim of the expedition was to study the deep Indonesian basins; a secondary goal was to investigate coral reefs and shallow seas. More details can be found in Weber (1902) and Van Aken (2005).

The zoological results of these explorations have been published in more than 100 monographs and papers, principally focusing on Porifera, Cnidaria, Decapoda, Amphipoda, Isopoda and Chaetognatha. Almost all material has been deposited in the Zoological Museum of Amsterdam; a complete list of the holdings is available on the Internet. The “errantiate” groups were studied by Horst (1903, 1912, 1913, 1917, 1918, 1919, 1921, 1924). Augener identified a number of new species in the beginning of the 20th century; his unpublished work was reviewed and partially published by Pettibone (1970). The “sedentariate” polychaetes were studied by Mesnil & Fauvel (1939) and by Caullery (1944), the pogonophores by Southward (1961) and the Siboglinidae by Caullery (1914) (named after the expedition). Hutchings & McRae (1993) more recently studied the Aphroditidae. A catalogue of published polychaete species found during the Siboga Expedition was compiled by Bleeker & van der Spoel (1992). Other significant taxonomic studies conducted in the region are those by Treadwell (1920) and Grube (1878) (for the Philippines), Pillai (1965) (Philippines & Indonesia), Fauvel (1939) (Indochina), Gallardo (1968) (Vietnam), and more recently, several papers by Eibye-Jacobsen (2002) (Andaman Islands) and Al-Hakim & Glasby (2004) (South China Sea). Notwithstanding the apparently large number of studies on this geographic area, our knowledge of the syllids in the region is sparse.

Although the Siboga syllids were previously identified by Augener, he became seriously ill in the course of his studies, which were never published. His identifications did not include any new syllids and, therefore, Pettibone (1970) did not include syllids

in her revision of new species identified by Augener. Funding by SYNTHESYS has now provided the chance to complete these studies, more than a century after they began.

Several more scientific expeditions have been organized to Indonesian waters, one of them, the Snellius II (1984). This campaign, carried out by the Dutch Research Vessel (RV) "Tyro" and the Indonesian RV "Samudera", collected additional material including syllids, which have been included in this present study. In addition, we have compared our specimens with a wide range of other material from other localities. Studies by two of us (MTA, GSM), focusing on the Syllidae fauna of Australia, has also provided comparative material. As might be expected, there is a high similarity between the syllid faunas of Australia and Indonesia. Where possible, specimens have been compared with type material, and with type material of other nominal species for diagnostic characters, especially, in the case of new species and records for Indonesia. Drawings have been made to illustrate new species; reinstated taxa, previously considered synonyms; difficultly identifiable taxa as well as two unnamed taxa of *Syllis*. These unnamed taxa probably represent new species, but since both are only represented by a single poorly preserved specimen, they are not formally named. In order to avoid damage to the old and unique material, only some specimens have been examined with scanning electron microscopy (SEM).

Techniques, equipment and conceptual theory have improved considerably since Augener began this study. In addition, the number of described taxa has increased markedly. This may partly explain the differences between earlier identifications and names given herein.

Material and Methods

A total of 32 samples have been studied (27 collected during the Siboga and 5 during the Snellius II Expedition). Material was collected from down to 420 m depth from Indonesia, fixed in a 4% formaldehyde-seawater and preserved in 70% alcohol. Most of the specimens were strongly pigmented in red. This feature, although described in each case, is not considered diagnostic; probably it is due to preservation processes rather than being a species-specific character. For identification, an Olympus SZ30 stereomicroscope and Olympus CH30 compound microscopes were used. Drawings were made to scale, with a camera lucida drawing tube in a Nikon Optiphotoptic

microscope equipped with interference contrast optics (Nomarsky). Specimens selected for scanning electron microscopy (SEM) were critical point dried and subsequently coated with 102 Å of gold. They were examined with a Philips XL30 electron microscope, connected to an EDAX DX4i analyzer at SIDI (Servicio Interdepartamental de Investigación), Universidad Autónoma de Madrid (UAM). Width of the specimens, excluding parapodia, was measured at the proventricle level. Unless stated otherwise, descriptions have been based on Indonesian material deposited in the Zoölogisch Museum, Universiteit van Amsterdam, Netherlands (ZMA) only. Comparative material has been lent by the Zoologisches Institut und Zoologisches Museum, Universität Hamburg, Germany (ZMH); Muséum Nationale d´Histoire Naturelle, Paris, France (MNHN), Zoologisches Museum, Museum für Naturkunde der Humboldt-Universität, Berlin, Germany (ZMB); the Australian Museum, Sydney, Australia (AM); Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt, Germany (FNS); Museo Nacional de Ciencias Naturales de Madrid, Spain (MNCN); Muzeum Przyrodnicze Wroclaw, Poland (MPW) and the Vitenskapsmuseet, Norges Teknisk-Naturvitenskapelige Universitet, Trondheim, Norway (NTNU).

We have included Augener identifications of the Siboga material in the section “material examined”.

Results

Thirty taxa of Syllidae in 10 genera have been identified. Four are new species: *Opisthosyllis mariae* n. sp., *Syllis komodoensis* n. sp., *Syllis villenai* n. sp. and *Syllis ypsiloides* n. sp. Two are new combinations: *Opisthosyllis flaccida* (Grube, 1878) and *Syllis setoensis* (Imajima, 1966). One species, *Syllis augeneri* Haswell, 1920, was previously considered a synonym of the nominal species *S. armillaris* (Müller, 1771), but has been recognised herein as a valid species and, is thus, re-described. Two *Syllis* taxa have been fully described but not named due to lack of well preserved material. Five more taxa have been questionably assigned to a specific name. Three of them, *Syllis* cf. *cornuta* Rathke, 1843, *S.* cf. *parapari* San Martín & López, 2000 and *S.* cf. *cruzi* Núñez & San Martín, 1991 agree with the diagnostic characters of the nominal species, but their reported localities are very disjunct; the material of *Paraehlersia* cf. *ehlersiaeformis* (Augener, 1913) is not well preserved; and *Branchiosyllis exilis* (Gravier, 1900) is identified as a possible complex.

Eusyllinae Malaquin, 1893

Genus *Eusyllis* Malmgren, 1867

Eusyllis Malmgren, 1867: 159. -San Martín, 2003: 112.

Type species. *Eusyllis blomstrandi* Malmgren, 1867.

***Eusyllis assimilis* Marenzeller, 1875**

Eusyllis assimilis Marenzeller, 1875: 158. - San Martín, 2003: 114-117, figs 52, 53. - San Martín & Hutchings, 2006: 273, figs 10a-j, 11a-e, 12a-c.

Material examined. 1 spec. ZMA V.Pol. 5254, Indonesia, NE coast of Sumba, 09°57'S 120°48'E, sandy bottom with sponges & gorgonians, 50 m, 1.2 m Agassiz trawl, Snellius II, Sta. 4.068, 16 Sept. 1984; 1 spec. AM W28942, Australia, New South Wales, SW side of South Solitary Is. 30° 12'S 153° 16'E, coral rubble, 18 m, 24 Jun. 1992; several spec. AM W28941, Western Australia, Red Bluff, Kalbarri, 27° 42'S 114° 09'E, mixed coralline algae on rocky shore, 3.5 m, 10 Jan. 1984. (Material from Australia identified by San Martín & Hutchings, 2006).

Remarks. The specimen agrees well with the previous descriptions and with material from Australia. The species was originally described from the Adriatic Sea (Mediterranean Sea), however, it was later found in different localities of the Atlantic and Pacific Ocean, and recently in the Indian Ocean (Australia).

Distribution. North Atlantic Ocean, Mediterranean Sea, North Pacific Ocean, South Pacific Ocean (New Zealand, Australia), Indian Ocean (Australia), Indonesia.

***Eusyllis lamelligera* Marion & Bobretzky, 1875**

Eusyllis lamelligera Marion & Bobretzky, 1875: 33. - San Martín, 2003: 117-120, figs 54, 55. - San Martín & Hutchings, 2006: 278, figs 15a-j, 16a-f.

Material examined. 1 spec. ZMA V.Pol. 5255, Indonesia, NE coast of Sumba, 09°57'S 120°49'E, sandy bottom and sponges, 45 m, Snellius II, Sta. 4.067, 16 Sept. 1984; 1 spec. AM W28960, Australia, New South Wales, N side of Bannister Head, N of Ulladulla, 35° 19.15'S 150° 29.12'E, grey sponge from top of boulder, 18 m, 6 May

1997; several spec. AM W28961, Western Australia, N end of Long Is. 28° 27.9'S 113° 46.3'E, dead coral substrate covered in coralline & brown algae, 5.5 m, 22 May 1994. (Material from Australia identified by San Martín & Hutchings, 2006).

Remarks. The specimen agrees well with the previous descriptions and with material from Australia.

Distribution. West Atlantic Ocean (North coast of the U.S.A. to Cuba), East Atlantic Ocean (from English Channel to Canary Islands), Mediterranean Sea, Pacific Ocean (Australia), Indian Ocean (Australia), Indonesia.

Genus *Odontosyllis* Claparède, 1863

Odontosyllis Claparède, 1863: 47. - San Martín, 2003: 101. - San Martín & Hutchings, 2006: 281-282.

Type species. *Syllis fulgurans* Audouin & Milne Edwards, 1833.

***Odontosyllis freycinetensis* Augener, 1913**

Odontosyllis freycinetensis Augener, 1913: 234, pl. II, fig. 7, text-figs 33 a, b. -Haswell, 1920: 107. - San Martín & Hutchings, 2006: 287-289, figs 23C-F, 24A-G, 25A-D.

Material examined. 1 spec. ZMA V.Pol. 5256, Indonesia, NE coast of Sumba, 09°57'S 120°48'E, sandy bottom with sponges & gorgonians, 50 m, 1.2 m Agassiz trawl, Snellius II, Sta. 4.068, 16 Sept. 1984; 1 spec. AM W28216, Australia, New South Wales, Manta Reef, North West Solitary Is., 30° 1.5'S 153° 16.5'E, lace bryozoan, 19 m, 25 Jun. 1992. (Material from Australia identified by San Martín & Hutchings, 2006).

Remarks. The specimen agrees well with the previous descriptions and with material from Australia.

Distribution. Indian Ocean (Western Australia), Pacific Ocean (Australia, New South Wales), Indonesia.

Genus *Paraehlersia* San Martín, 2003

Paraehlersia San Martín, 2003: 61.

Type species. *Ehlersia ferrugina* Langerhans, 1881, designated by San Martín, 2003.

Paraehlersia* cf. *ehlersiaeformis (Augener, 1913)

Material examined. 1 spec. ZMA V.Pol. 2222.01 (as *Syllis ferruginea* (sic)), Indonesia, anchorage between Timor and Nusa Besi, 8º25.2´S 127º18.4´E, 27-54 m, Siboga Expedition, Sta. 282, 15/17 Jan., 1900.

Remarks. Specimens in poor condition. A more accurate identification is not possible.

Distribution. Indonesia. Nominal species from Australia (all states).

Genus *Pionosyllis* Malmgren, 1867

Pionosyllis Malmgren, 1867: 158. - San Martín, 2003: 66.

Type species. *Pionosyllis compacta* Malmgren, 1867.

***Pionosyllis* sp.**

Material examined. 1 spec. ZMA V.Pol. 2222.02 (as *Syllis ferruginea* (sic)), Indonesia, Lesser Sunda Isl., Postillon Isl., anchorage of Pulu Sarassa, dredge, coral, 36 m, Siboga Expedition, Sta. 43, 4/5 March 1899; 1 spec. ZMA V.Pol. 5257, Indonesia, NE coast of Sumba, 09°57'S 120°49'E, sandy bottom and sponges, 45 m, Snellius II, Sta. 4.067, 16 Sept. 1984; 1 spec. ZMA V. Pol. 5258, Indonesia, Komodo, NE Cape, 08°29'S 119°34.1'E, sandy bottom with algae, occasional sponges and tunicates, 30-34 m, Snellius II, Sta. 4.096d, 19/20 Sept 1984.

Remarks. Specimens in poor condition. A more accurate identification is not possible.

Exogoninae Langerhans, 1879

Genus *Sphaerosyllis* Claparède, 1863

Sphaerosyllis Claparède, 1863: 45. - San Martín, 2003: 187, 188; 2005: 86, 87.

Type species. *Sphaerosyllis hystrix* Claparède, 1863.

***Sphaerosyllis georgeharrisoni* San Martín, 2005**

Sphaerosyllis georgeharrisoni San Martín, 2005: 97-99, figs 53, 54.

Material examined. Holotype AM W28657, Australia, West Australia: Goss Passage, Beacon Isl., 28º25.5'S 113º47'E, dead coral plates covered in coralline algae, 8 m, 22 May 1994; 1 spec. ZMA V.Pol. 2603 (as *Syllis* sp.), Indonesia, Maluku, Kajoa Isl., anchorage on E coast, townet, coral, 66 m, Siboga Expedition, Sta. 138, 3 Aug. 1899.

Remarks. The Indonesian specimen agrees with the holotype and the original description.

Distribution. Australia, Indonesia.

Syllinae Grube, 1850

Genus *Branchiosyllis* Ehlers, 1887

Branchiosyllis Ehlers, 1887: 148. - San Martín, 2003: 332.

Type species. *Branchiosyllis oculata* Ehlers, 1887.

Remarks. Branchiosyllis currently comprises 11 species. Six species are excluded for different reasons: *Branchiosyllis fuscosuturata* (Augener, 1922), *B. uncinigera* (Hartmann-Schröder, 1960) and *B. plessisi* (Rullier, 1972) have been considered synonyms of *B. exilis* by Westheide (1974), confirmed by other authors (Licher, 1999; San Martín *et al.*, submitted); *B. abranchiata* (Hartmann-Schröder, 1965) is not considered a valid species (it is a juvenile specimen: San Martín *et al.*, submitted) and *B. salina* (Hartmann-Schröder, 1959) probably should be transferred to *Opisthosyllis* Langerhans, 1879 (after examination of holotype, HZM P-14574).

***Branchiosyllis exilis* (Gravier, 1900)**

Figs 1, 2

?*Syllis (Typosyllis) exilis* Gravier, 1900: 160, figs 28-30.

Branchiosyllis exilis. - Westheide, 1974: 60-64, fig. 26.

Material examined. Holotype MNHN 143, Djibouti, Gulf of Aden; 1 spec. ZMA V.Pol.

1985.03, Indonesia, 8º30´S 119º7.5´E, 73 m, Siboga Expedition, Sta. 310, 12 Febr. 1900; 1 spec. ZMA V.Pol. 1985.05, Indonesia, Irian Jaya, Aru Isl., Pearl Banks, anchorage off Pulu Jedan, trawl, dredge and divers, sand and shells, 13m, Siboga Expedition, Sta. 273, 23/26 Dec. 1899; 4 spec. ZMA V.Pol. 1991, Indonesia, Irian Jaya, Aru Isl., Pearl Banks, anchorage off Pulu Jedan, trawl, dredge and divers, sand and shells, 13m, Siboga Expedition, Sta. 273, 23/26 Dec. 1899; 2 spec. ZMA V.Pol. 2038.03, Indonesia, Laboean, 8º44.5´ S 116º2.5´E, 18-27 m, Siboga Expedition, Sta. 19, 19 March 1899; 34 spec. (1 spec. mounted for SEM) ZMA V.Pol. 2038.01, Indonesia, Lesser Sunda Isl., Postillon Isl., anchorage of Pulu Sarassa, dredge, coral, 36 m, Siboga Expedition, Sta. 43, 4/5 March 1899. (All ZMA specimens previously identified as *Syllis exilis*).

Comparative material examined.

Branchiosyllis fuscosuturata (Augener, 1922). 2 syntypes, ZMB Verm. 6598; 1 syntype ZMH V-9770, Caribbean Sea, Tortugas, S.W. Channel and Bird Key riff.

Branchiosyllis cirropunctata (Michel, 1909). 2 spec. AM W30091, Australia, Western Australia: Goss Passage, Beacon Isl., 28°25' 30"S 113°47'E, dead plates of *Acropora* sp., covered in coralline algae, 8 m, 19 May 1994; 1 spec. AM W30092, NE entrance to Goss Passage, Beacon Isl., 28°27'54"S 113°46' 42"E, dead plate-like *Acropora* sp., covered in coralline algae, 8 m, 25 May 1994 (all identified by San Martín *et al.*, submitted).

Description. Best preserved specimen incomplete, with regenerating posterior part, 17.5 mm long, 0.8 mm wide, with 69 segments. Longest complete specimen 14 mm long, 0.8 mm wide and 64 segments. Body cylindrical, ventrally flattened. Reddish to orange pigmentation. Prostomium rounded; four eyes in open trapezoidal arrangement. Median antenna longer than combined length of prostomium and palps, inserted between anterior eyes, with about 22-30 articles; lateral antennae inserted on anterior margin of prostomium, shorter than median antenna (Fig. 1A), with about 17-23 articles. Palps similar in length to prostomium or slightly longer, ventrally folded. Peristomium shorter than subsequent segments; dorsal tentacular cirri similar in length to median antenna, with about 28-38 articles, ventral ones shorter than dorsal tentacular cirri (Fig. 1A), with about 18-23 articles. Dorsal cirri with distinct cirrophores. Dorsal cirri of chaetiger 1 long, with 53-58 articles; dorsal cirri of chaetigers two and three with 25-35 articles; 45-50 in chaetiger four; remaining anterior dorsal cirri varying in length but not clearly

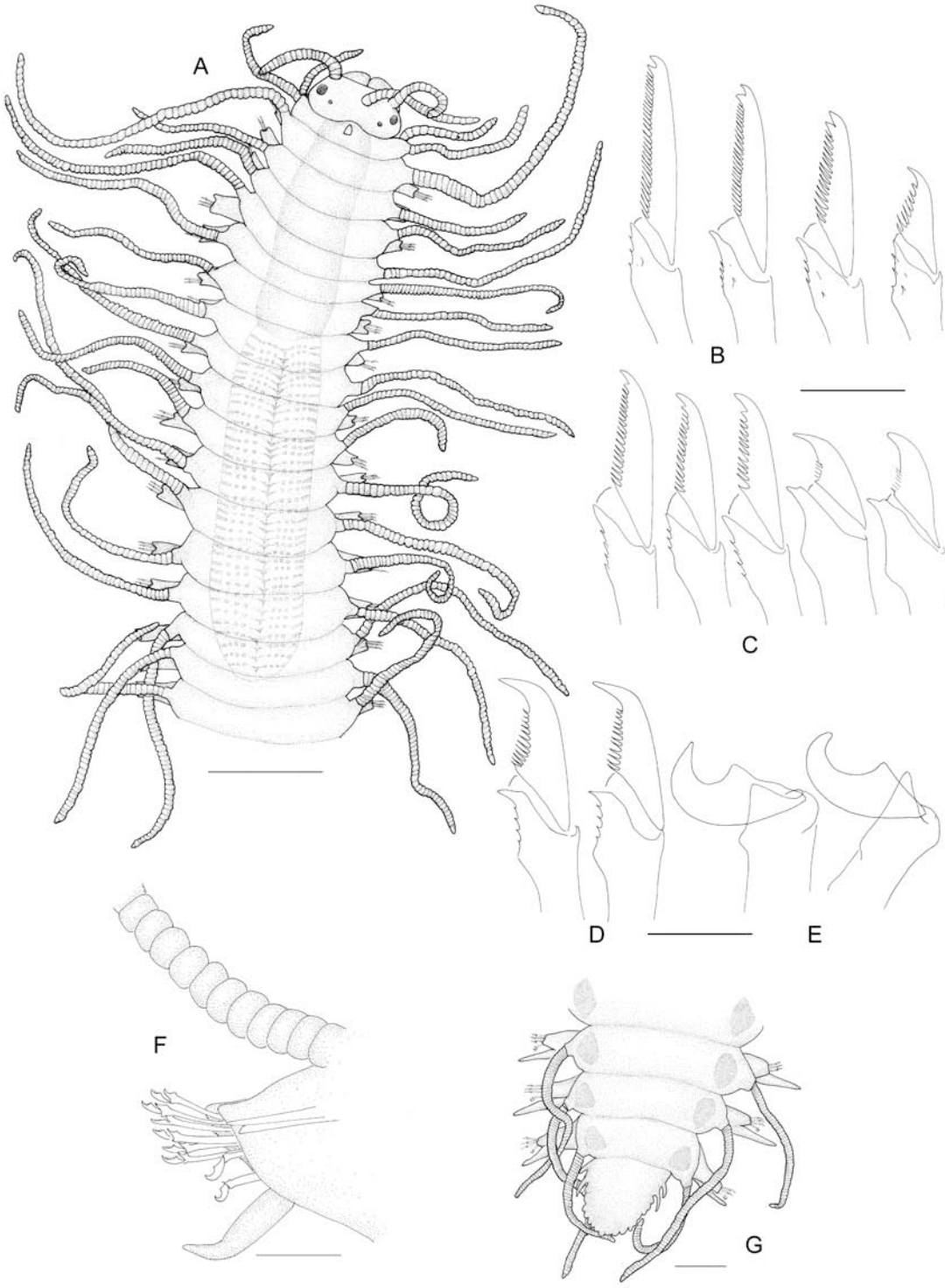

Figure 1. *Branchiosyllis exilis* ZMA V. Pol. 2038.01. A: Anterior part, dorsal view; B: Anterior chaetae; C: Midbody chaetae; D: Posterior chaetae; E: Posterior claw-shaped chaetae; F: Midbody parapodia, anterior view; G: Posterior part, dorsal view. Scale A: 0.5 cm.; B-D: 20 μm; F: 1 mm; G: 0.2 mm.

alternating (Fig. 1A), with 35-45 articles. Midbody dorsal cirri with about 40-50 articles, posterior cirri with 40-65. Parapodial lobes distally bilobed, prechaetal lobe shorter than postchaetal one, both digitiform (Fig. 1F). Ventral cirri digitiform, longer than parapodial lobes (Fig. 1F) and proximaly inserted to anterior parapodia; more distally inserted and increasing in length towards posterior segments, twice as long as parapodia (Fig. 1G). Usually six to ten compound heterogomph chaetae on anterior parapodia; blades falcigerous, bidentate, with long spines on margin, dorsoventrally decreasing in length (ca. 46 µm dorsal-most, ca. 24 µm ventral-most) (Figs 1B, 2A, B), shafts with distal spines. Midbody chaetigers with five to eight compound chaetae, three to six bidentate with shorter spines than anterior ones (ca. 39 µm dorsal-most, ca. 25 µm ventral-most), first two most ventral chaetae unidentate with spines only at base of blade, shafts with distal tip curved (Figs 1C, 2C). Dorsal chaetal shafts with distal spines, shafts of most ventral chaetae smooth (Fig. 1C). Bidentate chaetae becoming unidentate towards posterior end (Fig. 2D). In posterior chaetigers, first two blades of most ventral chaetae turn out 180º, becoming claw-shaped, with short, smooth shafts (Figs 1E, 2E, F); remaining six to seven chaetae with distally curved shafts with small spines, and hooked unidentate blades about 30 µm long, with long spines on edge (Fig. 1D). Anterior parapodia each with four slender aciculae, three straight, pointed, and one distally curving; from midbody posteriorly, number of aciculae per parapodium diminishes to two on posterior parapodia, one straight and pointed, the other slightly oblique at tip, both slightly protruding from parapodia. Pharynx through about six to eight segments; pharyngeal tooth located anteriorly, surrounded by crown of ten soft papillae. Proventricle longer than pharynx, through nine segments, with about 37 muscle cell rows, and distinct mid-dorsal line (Fig. 1A). Pygidium small, regenerating in most specimens, with two anal cirri similar to dorsal cirri (Fig. 1G). Some specimens with attached acephalous stolon, small, short, with about eight to ten chaetigers. Some specimens with dark oocytes laterally inside posterior segments (Fig. 1G).

Remarks. Branchiosyllis exilis, originally described from Djibouti, Gulf of Aden, is characterized by the presence of claw-shaped chaetae on posterior chaetigers, the most diagnostic character of the genus, and by the absence of branchiae, even though the generic name refers to the presence of branchiae. It is a widely distributed taxon, considered circumtropical, although material from different localities exhibits slight variations in some characters. The holotype unfortunately lacks all dorsal cirri.

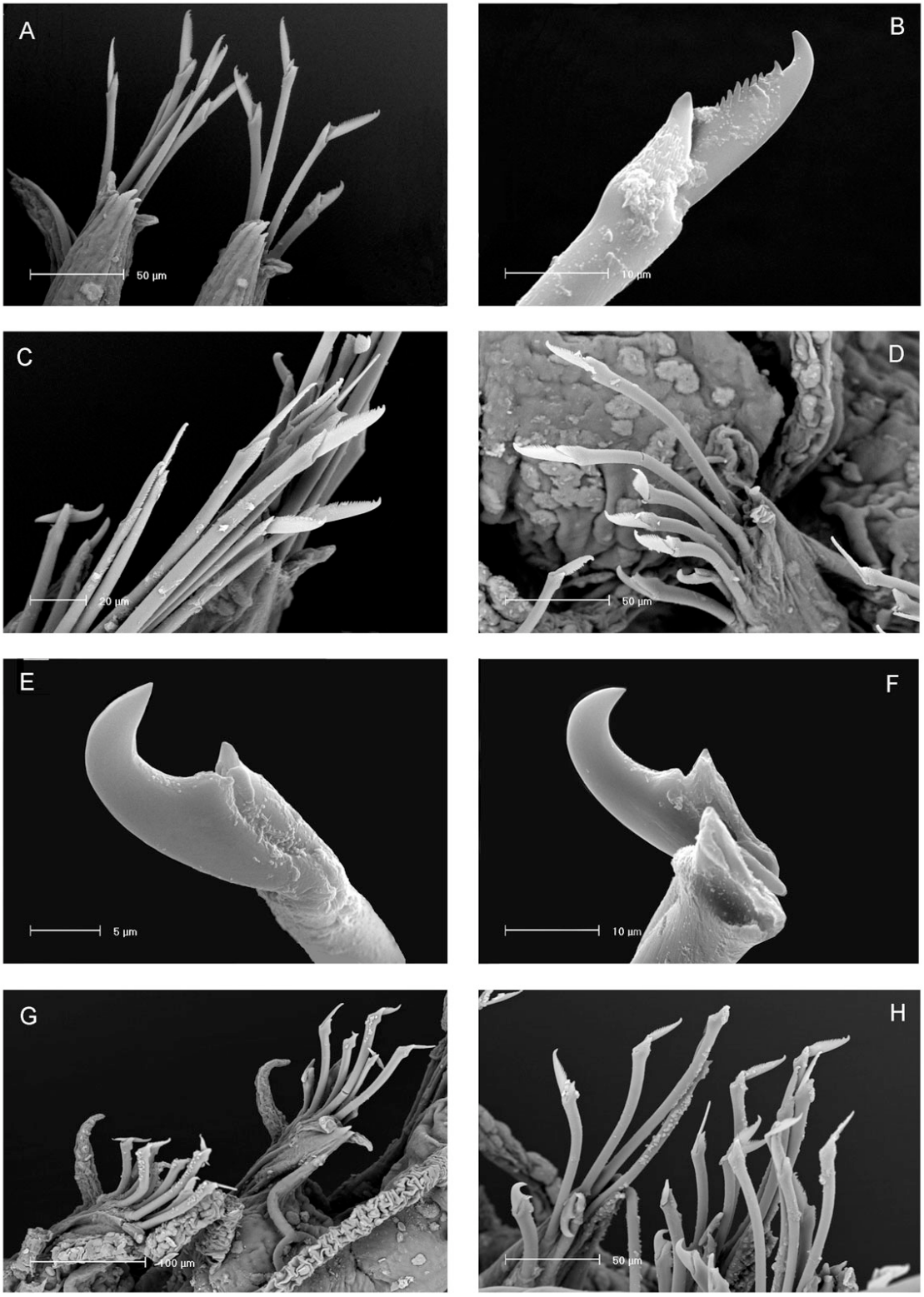

Figure 2. *Branchiosyllis exilis* ZMA V. Pol. 2038.01. SEM. A: Anterior parapodia, dorsal view; B: Anterior chaeta; C: Midbody chaetae; D: Midbody to posterior chaetae; E, F: Posterior claw-shaped chaetae; G: Posterior parapodia and ventral cirri, dorsal view; H: Posterior parapodia, ventral view.

Specimens from Indonesia largely agree with those described by Westheide (1974) from the Galapagos Islands. The latter specimens have long dorsal cirri (35-50 articles, as compared with 38-45 in Indonesia), while specimens from the Mediterranean (with approximately the same body length as those from Indonesia) identified as *B. exilis* (by San Martín, 2003) have shorter dorsal cirri (14-22 articles). Specimens from Indonesia have the fangs of the chaetae slightly curved in their distal part, while they are not curved in specimens from the Mediterranean, nor in the holotype. Westheide (1974) did not describe this character for specimens from the Galapagos. However, the examined types of *B. fuscosuturata* from the Caribbean Sea (synonymized with *B. exilis* by Westheide) present fangs slightly curved distally. Specimens from Indonesia present normal compound chaetae plus claw-shaped chaetae in the posterior chaetigers, while there are only claw-shaped chaetae in Mediterranean *B. exilis*. However, Indonesian specimens were regenerating their pygidiums and maybe such modified chaetae were present but these segments are now missing. In some of the examined Indonesian specimens, ventral cirri of posterior segments are distinctly long, twice as long as the parapodia; this feature has not been found in any description from other localities. In conclusion, there are many small differences between specimens identified as *B. exilis* around the world. A revision of all the material identified under this name will be necessary, as it may represent a complex of species. *Branchiosyllis cirropunctata* is a similar species but clearly differs in having dark spots on dorsal cirri and some details of chaetae.

Distribution. Apparently circumtropical, also present in the Mediterranean Sea.

***Branchiosyllis maculata* (Imajima, 1966)**

Figs 3, 4

Typosyllis maculata Imajima, 1966: 277, text-figs 59 a-m.

Branchiosyllis maculata. - Licher, 1999: 274. - San Martín *et al.*, submitted.

Material examined. 2 spec. (one spec. monted for SEM) ZMA V.Pol. 5259, Indonesia, NE coast of Sumba, 09°57'S 120°49'E, sandy bottom and sponges, 45 m, Snellius II, Sta. 4.067, 16 Sept. 1984; 1 spec. ZMA V.Pol. 5260, NE coast of Sumba, 09°57'S 120°48'E, sandy bottom, sponges and gorgonians, 50 m, 1.2 m Agassiz trawl, Snellius II, Sta. 4.068, 16 Sept. 1984; 4 spec. AM W30108, Australia, Western Australia,

inshore reef off Ned's Camp, Cape Range National Park, 21°59'S 113°59'E, frilly *Caulerpa* sp., 1m, 2 Jan. 1984; 3 spec. AM W29519, Australia, Western Australia, N end of beach, Bundegi Reef, 21°49'S 114°11'E, rocky rubble & brown alga with epiphytic growth, sticky sediment, 2m, 4 Jan. 1984; 2 spec. AM W30109, Australia, Western Australia, N end of beach, Bundegi Reef, Exmouth Gulf, 21°49'S 114°11'E, rocky rubble with sediment, brown alga with epiphytic growth, intertidal, 4 Jan. 1984; 3 spec. AM W30110, Australia, Western Australia, Goss Passage, Beacon Is., 28°25'30"S 113°47'E, dead plates of *Acropora* sp. covered in coralline algae, 8m, 19 May 1994. (Material from Australia identified by San Martín *et al.*, submitted).

Comparative material examined.

Branchiosyllis cirropunctata (Michel, 1909). 2 spec. AM W30091, Western Australia, Goss Passage, Beacon Isl., 28°25'30"S 113°47'E, dead plates of *Acropora* sp., covered in coralline algae, 8 m, 19 May 1994; 1 spec. AM W30092, NE entrance to Goss Passage, Beacon Isl., 28°27'54"S 113°46'42"E, dead plate-like *Acropora* sp., covered in coralline algae, 8 m, 25 May 1994 (all identified by San Martín *et al*., submitted).

Description. Longest specimen incomplete, 8 mm long, 0.7 mm wide, 58 segments. Body cylindrical, ventrally flattened. From proventricular segments backwards, one dorsal spot of black pigment on middle of each segment. Some articles of dorsal cirri partially black, usually two to three articles without pigment alternating with one pigmented (Fig. 3A). Prostomium rounded; four eyes in open trapezoidal arrangement, almost on line. Median antenna lost, insertion mark between posterior eyes. One lateral antenna lost, another with only one article, insertion on anterior margin of prostomium. One transversal ciliary band on prostomium, located anterior to eyes and median antenna (Fig. 4B). Palps triangular, longer than prostomium, fused at base, with a median groove. Peristomium short, considerably smaller than subsequent segments (Fig. 3A, 4A). Dorsal tentacular cirri with about 21 articles, ventral cirri shorter than dorsal ones, with about 14 articles. Dorsal cirri with distinct cirrophores. Dorsal cirri of chaetiger 1 long, with about 50 articles; subsequent most anterior dorsal cirri with 27-32 articles (Fig. 3A). Midbody and posterior dorsal cirri alternating long and short, with 36-39 and 21-24 articles respectively. Parapodial lobes distally bilobed, prechaetal and postchaetal lobes digitiform, similar in shape, postchaetal lobe slightly longer than prechaetal one (Figs 3I, 4E, F). Ventral cirri digitiform, proximally inserted, not exceeding beyond length of parapodial tip (Fig. 3I). Usually eight to nine compound

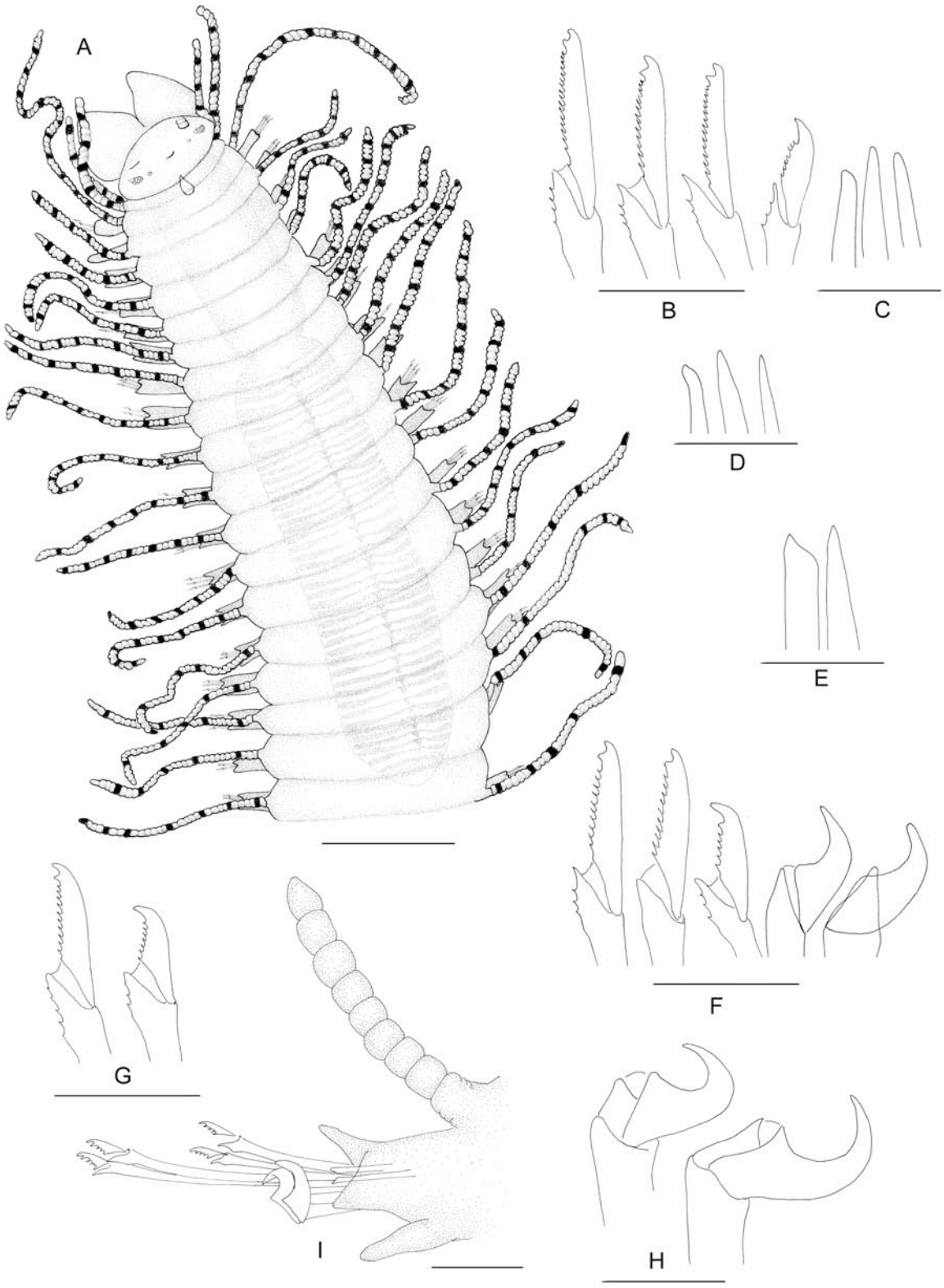

Figure 3. *Branchiosyllis maculata* ZMA V. Pol. 5260. A: Anterior part, dorsal view; B: Anterior chaetae; C: anterior aciculae; D: Midbody aciculae; E: Posterior aciculae; F: Midbody chaetae; G: Posterior chaetae; H: Posterior claw-shaped chaetae; I: Posterior parapodium, anterior view. Scale A: 0.5 mm; B-H: 20 μm; I: 48 μm.

heterogomph chaetae on anterior parapodia; blades falcigerous, bidentate, with spines on edge (Fig. 3B) and dorsoventrally decreasing in length (ca. 32.5 μm dorsal-most, ca. 19 μm ventral-most). Midbody parapodia with six to eight compound bidentate chaetae (ca. 30-15 μm), similar to those of anterior parapodia, except two to three most ventrally located with shorter shafts and short blades (ca. 20-25 μm). Dorsal-most blades with spines on edge, and long distal tooth (Figs 3F, 4D). Spines decreasing to lacking in ventral-most chaetae (Fig. 3F). Posterior chaetigers with six to eight compound chaetae, two to three most ventrally located with short shafts and claw-shaped blades, smooth on margin, unidentate and rotated 180º (Figs 3H, 4G, H); remaining four to five chaetae with longer shafts and bidentate blades (ca. 22-16 μm) (Fig. 3G). Anterior parapodia each with three slender aciculae, two straight and pointed and one slightly oblique at tip (Fig. 3C). Midbody and posterior segments with two to three aciculae protruding from parapodia, one to two straight and pointed, other slightly oblique at tip (Figs 3D, E, 4E, F). Pharynx through about seven segments; pharyngeal tooth located anteriorly, surrounded by crown of ten soft papillae. Proventricle longer than pharynx, through 12 segments, with about 43 muscle cell rows, and distinct mid-dorsal line (Fig. 3A). Pygidium missing.

Remarks. The specimens agree well with the original description of *B. maculata.* The claw-shaped chaetae, typical of *Branchiosyllis,* are difficult to observe in dorsal view, as their shafts are very short, sometimes appearing to be lacking. We compared specimens from Indonesia with those from Australia, and noticed some small differences in details of posterior chaetae: in Australian specimens, the bidentate chaetae are similar, but the proximal tooth is smaller than in specimens from Indonesia. The posterior chaetae in specimens from Indonesia have shafts not as curved in their distal parts, as occurs in specimens from Japan (cf. Imajima, 1966). However, shafts of Indonesian specimens are similar to those of specimens from Australia. These small differences may either be related to the geographic distances between populations or to the presence of a species complex, as postulated for *B. exilis.*

Branchiosyllis cirropunctata is a similar species, but it possesses claw-shaped chaetae only on its far posterior segments, and the chaetae have distinctly enlarged subdistal spurs on the head of the shaft.

Distribution. West Pacific Ocean (Southern Japan, Australia), Indonesia.

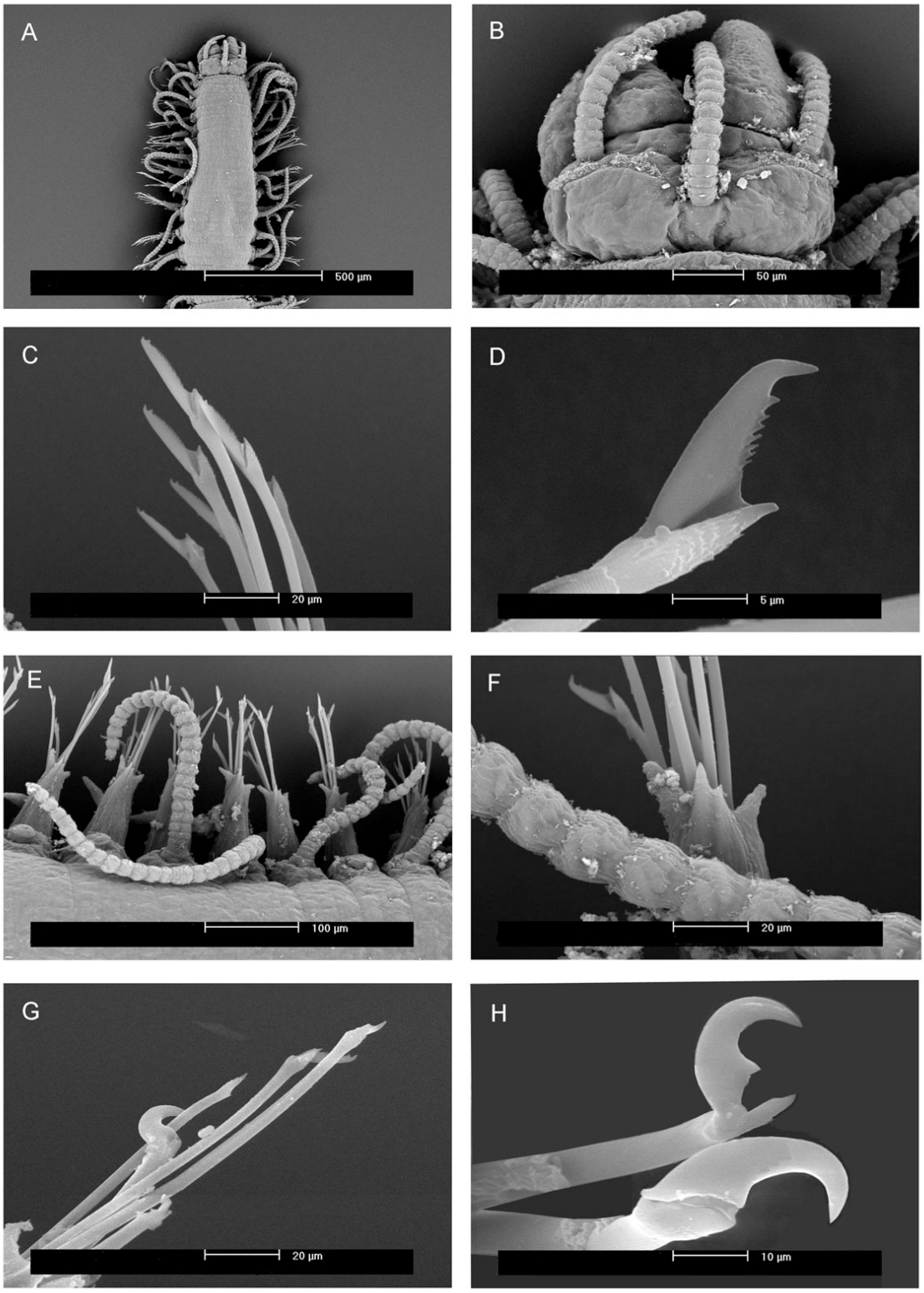

Figure 4. *Branchiosyllis maculata* ZMA V. Pol. 5259. SEM. A: Anterior part, dorsal view; B: Prostomium, dorsal view; C: Anterior chaetae; D: Midbody chaeta; E: Midbody parapodia, dorsal view; F: Midbody parapodium, dorsal view, midbody aciculae; G: Posterior chaetae; H: Posterior claw-shaped chaetae.

***Branchiosyllis verruculosa* (Augener, 1913)**

Fig. **5**

Syllis (Typosyllis) verruculosa Augener, 1913: 203, text-figs 24a-c, pl. 3, fig. 39.

Syllis verruculosa. - Monro, 1939: 29, text-fig. 298.

Branchiosyllis verruculosa. - Licher, 1999: 274. - San Martín *et al.*, submitted.

Material examined. 7 syntypes ZMB Verm. 5296, Australia, Western Australia, Albany; 4 syntypes ZMB Verm 5297, Australia, Western Australia, Shark Bay. 1 spec. ZMA V.Pol. 5261, Indonesia, NE coast of Sumba, 09°57'S 120°48'E, sandy bottom, sponges & gorgonians, 50 m, 1.2 m Agassiz trawl, Snellius II, Sta. 4.068, 16 Sept. 1984; 2 spec. AM W30129, Australia, SE end of Long Is., 28°28'48"S 113°46'30"E, dead coral substrate embedded in calcareous substrate, 30 m, 22 May 1994; 3 spec. AM W202642, Australia, Queensland, Triangular Islets, Shoalwater Bay, 22°23'S 150°30'E, 1981. (Material from Australia identified by San Martín *et al*., submitted)

Description. One incomplete specimen 4.5 mm long, 0.7 mm wide, with 33 segments. Body cylindrical, ventrally flattened. Dorsum irregularly pigmented with black spots on middle of some segments; scattered papillae laterally on each segment (Fig. 5A), more densely distributed from posterior segments to proventricle, some on ventrum. Segments with indistinct secondary annulation. Prostomium oval, proportionally large; four eyes in open trapezoidal arrangement, nearly on line. Median antenna slightly longer than combined length of prostomium and palps, located just in front of anterior eyes, with about 12 articles; lateral antennae inserted near anterior margin of prostomium, similar in length to median antenna, with about 12-14 articles. Palps shorter than prostomium, ventrally folded. Peristomium similar in length to subsequent segments; dorsal tentacular cirri with 21-26 articles, longer than median antenna; ventral ciri with 16-17 articles, shorter than dorsal ones (Fig. 5A). Dorsal cirri with about 20-26 articles. Parapodial lobes conical, distally bilobed, prechaetal and postchaetal lobes similar in size and length (Fig. 5G). Ventral cirri digitiform, shorter than parapodial lobes (Fig. 5G). About six to seven compound heterogomph chaetae on anterior parapodia; blades falcigerous, unidentate or indistinctly bidentate, with short spines on margin, decreasing in length dorsally to ventrally (ca. 30 μm dorsal-most, ca. 23 μm ventral-most) (Fig. 5B). Midbody parapodia with 10-11 compound chaetae, most dorsal blades similar to anterior ones (ca. 25-30 μm); two hooked chaetae located

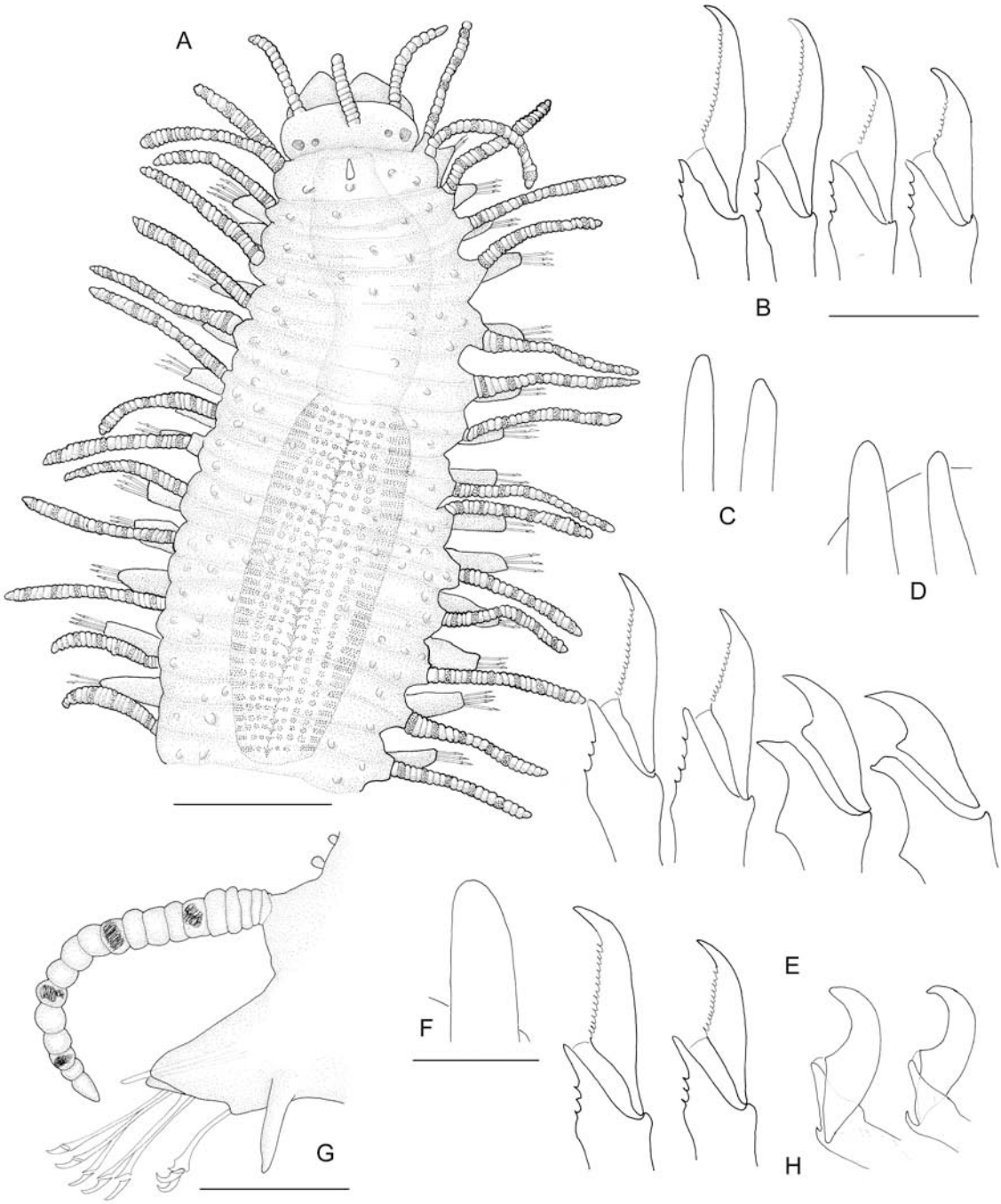

Figure 5. *Branchiosyllis verruculosa* ZMA V. Pol. 5261. A: Anterior part, dorsal view; B: Anterior chaetae; C: Anterior aciculae; D: Midbody aciculae; E: Midbody chaetae; F: Posterior acicula; G: Midbody parapodium, anterior view; H: Posterior chaetae. Scale A: 0.4 mm; B-F, H: 20 µm; G: 0.2 mm.

most ventrally on midbody fascicle, with small spines on edge or completely smooth (ca. 25 µm), with curved shafts (Fig. 5E). Towards posterior end, some blades become claw-shaped, with blades turned 180º. Posterior parapodia with two claw-shaped chaetae with curved shafts ending in two tips and seven chaetae similar to midbody ones (Fig. 5H). Anterior and midbody parapodia each with two slender and straight aciculae (Figs 5C, D); posterior segments with one single acicula in each parapodium, thicker than anterior ones and distinctly extending beyond parapodia (Figs 5F, G). Pharynx through about six to seven segments; pharyngeal tooth located anteriorly, surrounding papillae not observed. Proventricle longer than pharynx, through eight segments, with about 33 cell-rows and distinct mid-line (Fig. 5A). Pygidium lacking.

Remarks. Branchiosyllis verruculosa is the only species known within the genus with dorsal papillae. The specimen agrees well with the previous descriptions and with material from Australia.

Distribution. West and South Australia, Indonesia.

***Branchiosyllis* sp.**

Material examined. 1 spec. ZMA V.Pol. 5278 (ex ZMA V.Pol. 1985.03 as *Syllis exilis*), Indonesia, 8º30´S 119º7.5´E, 73 m, Siboga Expedition, Sta. 310, 12 Febr. 1900.

Remarks. The specimen is in poor condition and cannot be identified to species.

Genus *Haplosyllides* Augener, 1924

Haplosyllides Augener, 1924: 44.

Type species. *Haplosyllides floridana* Augener, 1924

***Haplosyllides* sp.**

Material examined. 2 spec. ZMA V. Pol. 5280 (ex ZMA V.Pol. 2046 as *Syllis zonata*), Indonesia, anchorage off Pulu Tongkil, Sulu Archipelago, 13 m, Siboga Expedition, Sta. 109, 5/6 July 1899; 4 spec. ZMA V.Pol. 5271, Indonesia, NE coast of Sumba, 09°57'S 120°48'E, sandy bottom, sponges and gorgonians, 50 m, 1.2 m Agassiz trawl, Snellius II, Sta. 4.068, 16 Sept. 1984.

Remarks. This genus is currently being revised and will be published later.

***Genus Opisthosyllis* Langerhans, 1879**

Opisthosyllis Langerhans, 1879: 541. - San Martín, 2003: 329.

Type species. *Opisthosyllis brunnea* Langerhans, 1879

***Opisthosyllis flaccida* (Grube, 1878) n. comb.**

Fig. 6

Syllis flaccida Grube, 1878: 118-119 + p. 112, Pl. 7, fig. 6.

Typosyllis flaccida. - Licher, 1999: 246, 247, fig. 103.

Material examined. 3 Syntypes MPW 394, 2 Syntypes ZMB Q 4395, Philippines, Camiguin, Aibuhit. 2 spec. ZMA V.Pol. 1985.04 (as *Syllis exilis*), Indonesia, Lesser Sunda Isl., Bay of Bima, near south fort, trawl, dredge, muddy bottom with coral sand, 55 m, Siboga Expedition, Sta. 47, 8/12 April 1899.

Comparative material examined.

Opisthosyllis leslieharrisae Aguado, San Martín & Nygren, 2005. Type material MNCN 16.01/10264-66, USA, California, Santa Catalina Island, Wrighley Marine Science Centre, 1-4 m, 33˚26.7'N 118˚29.1'W.

Description. Largest syntype 37 mm long, 1.5 mm wide, with 121 segments. Specimens from Indonesia 27 mm long, 1.2 mm wide with 82 segments; 32 mm, 1.3 mm, 77 segments, respectively. Body broad and flaccid. Segments slightly annulated secondarily, with about four to five rings. Dorsal surface covered by small irregularly distributed dark inclusions (Fig. 6A). Prostomium wider than long, rectangular to oval, with two pairs of dark eyes in trapezoidal arrangement, anterior pair larger than posterior, eye spots absent. Palps broad, fused at base, with central groove, similar in length to prostomium, ventrally folded. Antennae, tentacular and dorsal cirri distinctly thick. Median antenna with 20 articles. Lateral antennae inserted on anterior margin of prostomium, slightly shorter than median antenna, with 16 articles. Triangular occipital flap partially covering posterior part of prostomium. Peristomium shorter than subsequent segments (Fig. 6A). Dorsal tentacular cirri with 32-35 articles, ventral pair shorter, with 20 articles. Anterior dorsal cirri with 21-24 articles, midbody and posterior dorsal cirri with 25 articles. Ventral cirri digitiform, inserted proximally, reaching tip of

parapodia (Fig. 6H). Prechaetal and postchaetal lobes similar in length, on all parapodia. Seven heterogomph compound chaetae on anterior chaetigers, nine to ten on median and five to seven on posteriorly-most parapodia. Compound chaetae of anterior and midbody parapodia with slightly bidentate blades, proximal tooth small. Blade edge with short spines; distal part of shafts provided with minute spines (Figs 6B, C). Length of dorsal-most chaetal blades on anterior parapodia and midbody parapodia ca. 30 μm. Posterior compound blades unidentate, ca. 26 μm long, with short spines; shafts distally curved (Fig. 6D). Dorsal and ventral simple chaetae not seen. Four straight aciculae in anterior parapodia, three in median and two in posterior, all straight or slightly oblique (Figs 6E, F). Pygidium conical (Fig. 6G), two anal cirri with about 30 articles. Pharynx through eight segments, similar in length but somewhat narrower than proventricle, tooth long and slender, dagger-shaped, located on midline of pharynx. Proventricle through segment 9 to 14, rectangular to oval, with about 30 rows of muscular cells (Fig. 6A). Both specimens from Indonesia developing female stolons (oocytes accumulated in last 22, and 30 segments, respectively).

Remarks. The description above is based on the Indonesian material; the syntypes are longer and exhibit some variations in number of articles of antennae and dorsal cirri (median antenna 26-30 articles, lateral ones 18-22, tentacular cirri 40-45, dorsal cirri of anterior segments 25-35, midbody cirri 30-40 and posterior ones 25-28). A pharyngeal tooth located posteriorly in the pharynx is the principal diagnostic character for *Opisthosyllis* and is visible, after dissection, in both the types and Indonesian material. The shape of the compound chaetae and presence of an occipital flap in *O. flaccida* are also other diagnostic characters of *Opisthosyllis*. Other species with a tooth in the middle of the pharynx are *Opisthosyllis laevis* Day, 1957, *O. longidentata* San Martín, 1991 and *O. leslieharrisae*. In contrast to *O. flaccida*, *O. laevis* have bidentate falcigers; *O. longidentata* has thin dorsal cirri becoming pseudoarticulated in the posterior part of the body and bidentate blades with long spines and, finally, *O. leslieharrisae* has papillae over the dorsum and bidentate blades with long spines (Day, 1957; San Martín, 1991; Aguado *et al.*, 2005).

Distribution. Philippines, Indonesia.

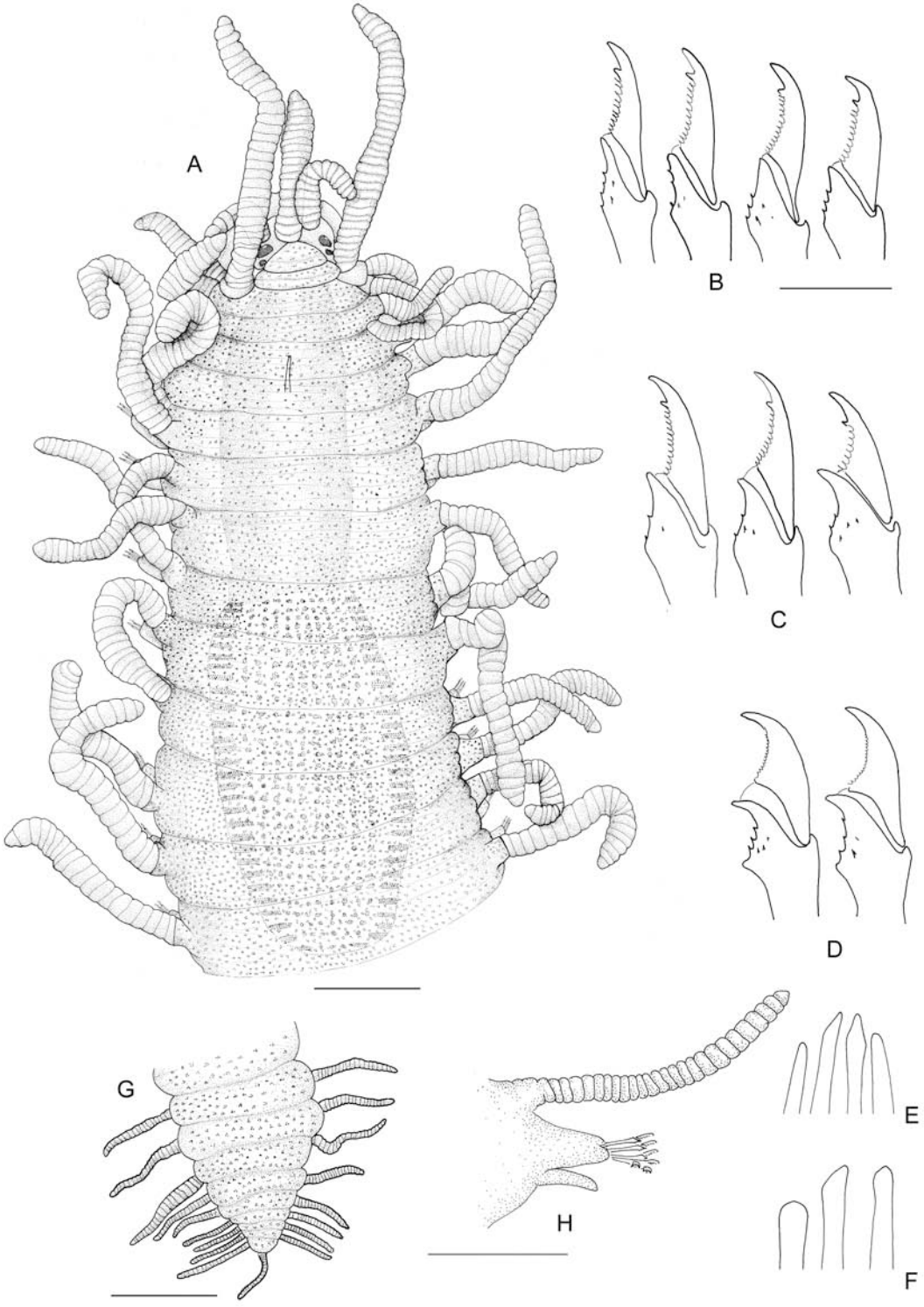

Figure 6. *Opisthosyllis flaccida* n. comb. ZMA V. Pol. 1985.04. A: Anterior part dorsal view; B: Anterior chaetae; C: Midbody chaetae; D: Posterior chaetae; E: Anterior aciculae; F: Midbody aciculae; G: Posterior part, dorsal view; H: Parapodium, anterior view. Scale A: 0.5 cm; B-F: 30 µm; G: 1.4 cm; H: 1 mm.

***Opisthosyllis mariae* n. sp.**

Fig. 7

Material examined. Holotype ZMA V.Pol. 1985.02, Indonesia, Sula Besi Isl., E coast, Sanana Bay, reef expl., 22m, muddy bottom, Siboga Expedition, Sta. 193, 13/14 Sept. 1899; 1 paratype ZMA V.Pol. 2038.02, Indonesia, Maluku, Banda anchorage, trawl, dredge, reef expl., 9-45 m, black sand and coral, Siboga Expedition, Sta. 240, Nov. 22 Dec. 1899. (Both specimens as *Syllis exilis*).

Comparative material examined

Opisthosyllis papillosa Hartmann-Schröder, 1960. 4 Paratypes P-14718-ZMH, Red Sea, Schab Anbar, Ghadarqa, *Pocillopora*, 1.5 m.

Opisthosyllis australis Augener, 1913. 3 syntypes HZM V-7947, Western Australia, Shark Bay, 25º47’59.60’’S 113º40’32.53’’E; 1 syntype ZMB 53081, SW Australia, Freemantle, Rottnest, 31º59’29.85’’S 115º39’08.82’’E.

Opisthosyllis leslieharrisae. Holotype MNCN 16.01/10264 and paratypes MNCN 16.01/10265-66, USA, California, Santa Catalina Island, Wrighley Marine Science center, 33˚26.7’N 118˚29.1’W, 1-4 m.

Description. Holotype 13.5 mm long, 1 mm wide, with 89 chaetigers. Paratype 22 mm long, 0.9 mm wide, with 84 chaetigers. Body circular, ventrally flattened; body width fairly constant, with tapering ends. Both specimens strongly pigmented red. Dorsal surface covered with spherical papillae distributed in two to three irregular transversal rows per segment (Fig. 7A). Papillae absent on parapodia. Prostomium wider than long, rectangular to oval, with two pairs of dark eyes, in trapezoidal arrangement; eye spots absent. Palps broad, fused at base, with distinct central groove; similar in length to prostomium, ventrally folded. Median antenna lost, insertion mark located medially on prostomium. Lateral antennae inserted on anterior margin of prostomium, with 10-12 articles. Occipital flap lacking. Peristomium shorter than subsequent segments (Fig. 7A). Dorsal tentacular cirri with 23-26 articles, ventral pair shorter, with 12-19 articles. Anterior dorsal cirri with 15-22 articles, midbody dorsal cirri alternating in length with 14-20 articles, longer ones inserted more dorsal and pointing up and shorter ones inserted more ventral and pointing down or laterally. Posterior dorsal cirri with 14-16 articles. Cirrophores well developed (Fig. 7I). Basal articles narrow, increasing in width and length in middle of cirri, becoming shorter and narrower distally (Fig. 7I). Ventral

cirri conical, proximally inserted and not extending beyond parapodial tips. Pre- and postchaetal lobes present on all parapodia, the latter lobes longer than prechaetal on anterior parapodia, with one distal papilla; both lobes equal in length on posterior parapodia. Chaetal fascicle with three to four heterogomph compounds on anterior chaetigers, five to six on midbody and posteriorly. On anterior and middle parapodia, compound chaetae with unidentate blades with short spines on edge, distal part of shafts also with small spines (Figs 7B, D). Length of dorsal-most chaetal blades ca. 30 μm on anterior parapodia, and ca. 26 μm on median parapodia. On posterior chaetigers, compound chaetae with curved unidentate blades, smooth on margin (ca. 26 μm); shafts with two tips, distally curved (Fig. 7F). Dorsal and ventral simple chaetae not seen. Three aciculae in anterior parapodia protruding from parapodial lobes (Fig. 7C), three in median and posterior segments, one slightly curving at tip, all distally blunt (Figs 7E, G). Pygidium in both specimens regenerating; anal cirri absent (Fig. 7H). Pharynx shorter than proventricle, almost as broad as proventricle. Large conical tooth located in posterior part of pharynx. Proventricle long, rectangular, through segment 8 to 16, cell-rows difficult to distinguish (Fig. 7A). Paratype developing a stolon of 21-22 segments.

Remarks. *Opisthosyllis mariae* n. sp., is characterised by having a body surface covered by spherical papillae, unidentate blades from midbody to posterior end and posterior shafts distally curved. There are currently five other species described within *Opisthosyllis* with papillae over the dorsum, *O. viridis* Langerhans, 1879; *O. australis* Augener, 1913; *O. papillosa* Hartmann-Schröder, 1960; *O. convexa* Lee & Rho, 1994 and *O. leslieharrisae* Aguado, San Martín & Nygren, 2005. Aguado *et al*. (2005) concluded that the type material of *O. australis* from ZMH did not exhibit any papillae. However, revision of types of the same species deposited in the ZMB reveal this character to be present, but papillae are badly preserved in the ZMH type. All five species have compound chaetae with clear bidentate blades, while blades in *O. mariae* are unidentate. In addition, *O. viridis*, *O. papillosa, O. australis* and *O. convexa* have conical papillae considerably smaller than the spherical ones of *O. mariae*. *Opisthosyllis leslieharrisae* has bigger papillae, present in two sizes (Aguado *et al*., 2005). In addition, shafts of posterior chaetae in *O. mariae* are distally curved, with two tips. This combination of characters is not present in any other *Opisthosyllis* species as described by Augener (1913), Hartmann-Schröder (1960), Lee & Rho (1994), López & San Martín (1994) and in our observations. A table comparing species of *Opisthosyllis* is

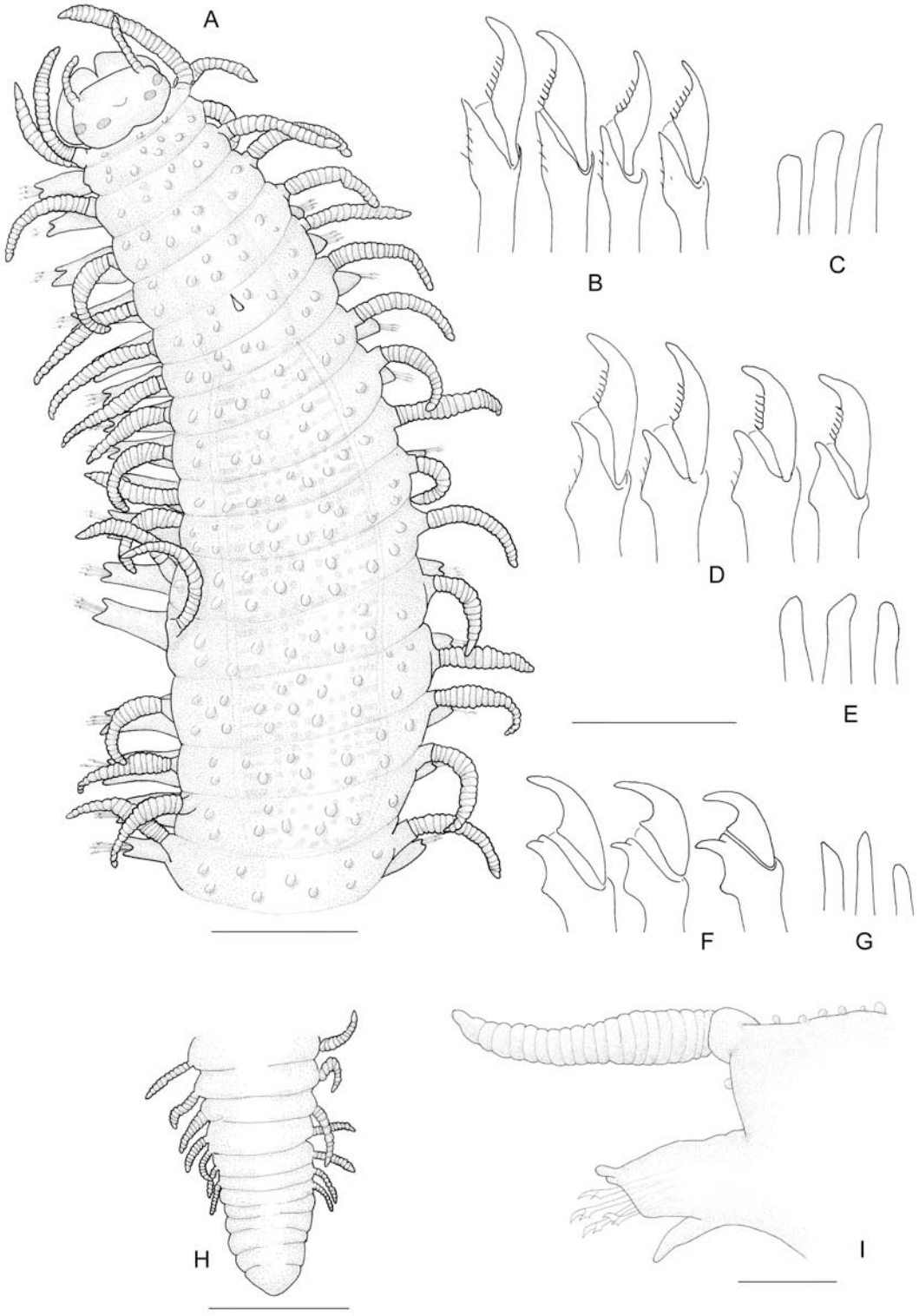

Figure 7. *Opisthosyllis mariae* n. sp. Holotype V. Pol. 1985.02. A: Anterior part, dorsal view; B: Anterior chaetae; C: Anterior aciculae; D: Midbody chaetae; E: Midbody aciculae; F: Posterior chaetae; G: Posterior aciculae; H: Posterior part, dorsal view; I: Midbody parapodium, posterior view. Scale A, H: 0.5 cm; B-G: 30 µm; I: 1mm.

given in Aguado *et al.* (2005).

Distribution. Indonesia.

Etymology. This species is named after our colleague and good friend María Capa for her valuable contributions to the taxonomy of polychaetes and her inestimable friendship.

Genus *Syllis* Lamarck, 1818

Syllis Lamarck, 1818: 318. - San Martín, 1992: 168-170; 2003: 336-341.
Type species. *Syllis monilaris* Lamarck, 1818

Remarks. Syllis is one of the taxonomically most difficult genera within the Syllidae due to the high diversity, lack of detailed descriptions and confusion in the generic nomenclature (San Martín, 1992). The genus currently comprises more than 130 species and is not homogeneous (San Martín, 2003), so further revisions are necessary. Following other authors (San Martín, 1984, 1992, 2003; Licher, 1999), subgenera are not accepted herein and *Typosyllis* is considered a synonym of *Syllis* (San Martín, 2003).

***Syllis aciculata* Treadwell, 1945**

Syllis aciculata Treadwell, 1945: 1, 2, figs 1-5. - Díaz-Castañeda & San Martín, 2001: 710.
Typosyllis aciculata. - Licher, 1999: 92-94, fig. 44.

Material examined. 1 spec. ZMA V.Pol. 2202 (as *Syllis variegata),* Indonesia, Sulawesi, Kwandang Bay, E side of Pajunga Isl., reef, Siboga Expedition, Sta. 115, 9/11 July 1899.

Remarks. The specimen agrees well with the previous descriptions.

Distribution. Pacific Ocean (California to Panamá, South China Sea), Indonesia.

***Syllis alternata* Moore, 1908**

Syllis alternata Moore, 1908: 323. - San Martín, 2003: 354-358, figs 192, 193.
Typosyllis alternata. - Licher, 1999: 253-255, fig. 106.

Material examined. 1 spec. ZMA V.Pol. 2019.04 (as *Syllis variegata*), Indonesia, Irian Jaya, Aru Isl., Pearl Banks, anchorage off Pulu Jedan, trawl, dredge and divers, sand and shells, 13m, Siboga Expedition, Sta. 273, 23/26 Dec. 1899. 1 spec. ZMA V.Pol. 5282, Indonesia, Komodo, NE Cape, 08°29'S 119°34.1'E, sandy bottom, algae and occasional sponges and tunicates, 30-34 m, Snellius II, Sta. 4.096, 19/20 Sept. 1984.

Remarks. The specimens agree well with the previous descriptions.

Distribution. North Pacific Ocean (from Alaska to Panama, Japan), Chuckchi Sea. Atlantic Ocean (U.S.A.), Caribbean Sea, Mediterranean Sea, Indonesia.

***Syllis armillaris* (Müller, 1771)**

Nereis armillaris Müller, 1771: 150.
Syllis brachychaeta Schmarda, 1861: 70.
Syllis closterobranchia Schmarda, 1861: 72.
Syllis (Typosyllis) armillaris. - Fishelson & Rullier, 1969: 60.
Typosyllis armillaris. - Licher, 1999: 189-199, fig. 84.
Syllis armillaris. - San Martín, 2003: 423-426, figs 232, 233.

Material examined. 1 spec. ZMA V.Pol. 2227.01 (as *Syllis brachychaeta*), Indonesia, Lesser Sunda Isl., anchorage E of Dangar Besar, Saleh Bay, dredge, trawl, reef expl., sand, coral, muddy bottom, down to 36 m, Siboga Expedition, Sta. 313, 14/16 Febr. 1900; 1 spec. ZMA V.Pol. 2227.02, 7º15´S 115º15.6´E, trawl, mud and broken shells, 289 m, Siboga Expedition, Sta. 12, 14 March 1899.
Comparative material examined.
Syllis armillaris. Several spec. MNCN 16.01/7906-07, Spain, Almería, Cabo de Gata, 2 m, 36º46’49.11’’N 2º14’25.31’’W, Jan. 1987. (Identified by San Martín, 2003).

Remarks. The specimen agrees well with the previous descriptions, although the presence of slight differences in populations from different geographical locations

suggested that it might be a complex of species (San Martín, 2003). *Syllis brachychaeta* and *S. closterobranchia* were synonymized by Augener (1927, and then used in his unpublished manuscript on the Siboga material), later both were synonymized with *S. armillaris* by Fauvel (1955), Day (1954, 1967) and Fishelson & Rullier (1969).

Distribution. Apparently cosmopolitan.

***Syllis augeneri* Haswell, 1920**

Fig. **8**

Syllis (Typosyllis) augeneri Haswell, 1920: 98-99, pl. 11, figs 19-22

Material examined. 1 syntype AM W 505, Australia, New South Wales, Port Jackson, 33º51'S 151º16'E; 1 spec. ZMA V.Pol. 2019.05 (ex ZMA V.Pol. 2019.04 as *Syllis variegata*), Indonesia, Irian Jaya, Aru Isl., Pearl Banks, anchorage off Pulu Jedan, trawl, dredge and divers, sand and shells, 13m, Siboga Expedition, Sta. 273, 23/26 Dec. 1899.
Comparative material examined.
Syllis armillaris. Several spec. MNCN 16.01/7906-07, Spain, Almería, Cabo de Gata, 2 m, 36º46'49.11''N 2º14'25.31''W, Jan. 1987. (Identified by San Martín, 2003).

Description. Incomplete specimen, 7 mm long, 0.5 mm wide, with 43 segments. Prostomium wider than long, with two pairs of eyes in trapezoidal arrangement, posterior ones slightly larger than anterior, two eyespots located anteriorly (Fig. 8A). Median antenna lost, insertion mark on middle of prostomium; short lateral antennae inserted on anterior margin of prostomium, shorter than combined length of prostomium and palps, with 9-11 articles. Palps broad, triangular, slightly longer than prostomium, fused at base, with distinct median groove. Peristomium similar in length to subsequent segments, with two pairs of tentacular cirri (Fig. 8A). Dorsal tentacular cirri longer than lateral antennae, with 11-12 articles, ventral ones with 10-11 articles. Pre- and postchaetal lobes present in all parapodia, both similar in length (Fig. 8I). Dorsal cirri short, with 12-13 articles, dorsal cirri of first chaetiger slightly longer, with 18 articles. Ventral cirri digitiform, inserted proximally, not extending beyond parapodial lobes (Fig. 8I). Anterior parapodia each with 10-15 compound, heterogomph chaetae, distal part of shafts provided with spines, bidentate blades, four most dorsal blades longer (ca. 26-28 μm), remaining shorter (ca. 15 μm), distal tip of blades curved, with distal tooth

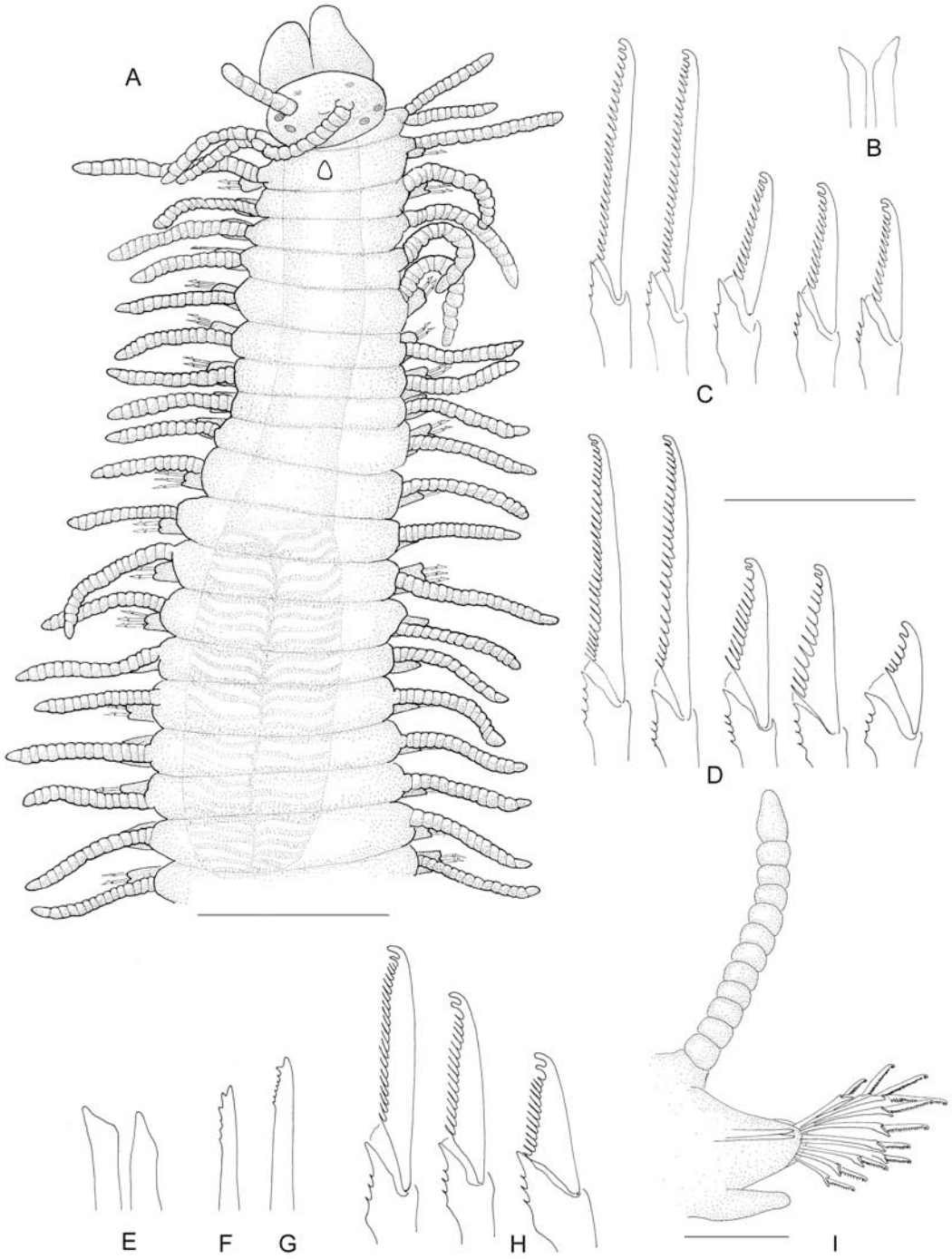

Figure 8. *Syllis augeneri* ZMA V. Pol. 2019.05. A: Anterior part, dorsal view; B: Anterior aciculae; C: Anterior chaetae; D: Midbody chaetae; E: Posterior aciculae; F: Ventral simple chaetae; G: Dorsal simple chaeta; H: Posterior chaetae; I: Midbody parapodium, anterior view. Scale A: 0.4 mm; B-H: 20 μm; I: 1 mm.

longer than proximal one and spines on edge (Fig. 8C). Midbody chaetigers with 9-10 compound chaetae, bidentate blades slightly shorter in length than those of anterior parapodia, two dorsal-most blades longer (ca. 27.2 μm), remaining gradually decreasing in length (ca. 18-12 μm) (Fig. 8D). Posterior chaetigers with six compound bidentate chaetae, decreasing in length (ca. 26 μm dorsal-most, ca. 12 μm ventral-most), similar in shape to anterior ones (Fig. 8H). Posterior chaetigers with one dorsal simple chaetae unidentate with large spine located laterally (Fig. 8G), and one bidentate ventral simple chaeta with spines on margin (Fig. 8F). Two acuminate aciculae per parapodium, one of them slightly protruding (Figs 8B, E). Pygidium lost. Pharynx long, extending through 11 segments; conical tooth on anterior margin. Proventricle extending through eight segments, with 27 cell-rows and one median longitudinal line (Fig. 8A). Male stolon in development.

Remarks. Syllis augeneri was described from Port Jackson, Australia and was synonymized by Licher (1999) with *Syllis armillaris*, a cosmopolitan species (although probably a complex of different species). After studying the syntype and material from Indonesia, we are of the opinion that there are enough differences to maintain *S. augeneri* as a valid species. Dorsal cirri are similar in length and shape to those of *S. armillaris*, but the distal end of the chaetae, with both teeth markedly curved, the long spines and the bilobed parapodia are distinctly different.

Distribution: Australia (New South Wales), Indonesia.

***Syllis* cf. *cornuta* Rathke, 1843**

Fig. 9

*Material examined***.** 1 spec. ZMA V.Pol. 2211.02 (as *Syllis sexoculata*), Indonesia, 6º8´N 121º19E, 275 m, Siboga Expedition, Sta. 105, 4 July 1899.

Comparative material examined

Syllis cornuta Rathke, 1843. 5 Neotypes (NTNU 410-415). Norway, Trondheimsfjorden, Bergensfjorden (designed by Licher, 1999).

Description. Incomplete specimen, 9 mm long, 0.8 mm wide, with 68 segments. Body strongly pigmented, dark red. Prostomium wider than long, with two pairs of eyes in

trapezoidal arrangement, anterior ones larger than posterior. Median antenna inserted on middle of prostomium, broken, with 18 articles. Lateral antennae anteriorly inserted, equal to combined length of prostomium and palps. Palps triangular and broad, longer than prostomium, fused at base, with distinct median groove. Peristomium shorter than subsequent segments (Fig. 9A). Dorsal tentacular cirri with 23 articles, ventral tentacular cirri shorter, with 15 articles. Anterior dorsal cirri with 15-20 articles not showing clear variation in length, midbody dorsal cirri clearly alternating in length, long ones with 20-25 articles and short ones with 13-15. Ventral cirri conical, proximally inserted, exceeding parapodial lobes in length (Fig. 9H). Anterior chaetigers with 15 compound heterogomph chaetae. Four dorsal-most blades longer than remaining (ca. 60-75 μm), pseudospiniger, bidentate, with fine spines along blade edge, blades of remaining chaetae dorsoventrally decreasing in length (ca. 40 μm dorsal-most, ca. 25 μm ventral-most) (Fig. 9C). Midbody parapodia with 18 compound chaetae, two to four pseudospinigers located most dorsally, and remaining falcigers, both similar in length to anterior ones. Posterior chaetigers with 13-18 compound chaetae, dorsal-most pseudospiniger (ca. 75 μm), remaining falcigers shorter than those from anterior chaetigers (ca. 24-40 μm) (Fig. 9G). Dorsal simple chaetae unidentate, straight, distally with small spines (Fig. 9E). Sigmoid, bidentate ventral simple chaetae on posterior parapodia (Fig. 9D). Anterior chaetigers with four straight, pointed aciculae (Fig. 9B), posterior chaetigers with two, one larger and slightly protruding from parapodia (Fig. 9F). Pygidium missing. Pharynx long, similar in length to proventricle, with ten distal papillae, quadrangular in shape. Pharyngeal tooth anteriorly located. Proventricle long, extending through 12 segments, number of cell-rows not distinguishable, as insufficient transparency (Fig. 9A).

Remarks. The specimen agrees with most of the characters of *S. cornuta*, except for the length of dorsal cirri and segments width, as given by Rathke (1843) and Licher (1999). Dorsal cirri and segments are shorter in the Indonesian specimen; however, the size of our specimen is considerably smaller (9 mm) than the neotype (30 mm). *Syllis cornuta* was described from Norway and there are many subsequent reports of this species all around the world including Japan and Australia. Licher (1999) revised a large amount of material from different geographical areas, concluding that some reports were dubious. However, our unique specimen does not have any external feature sufficiently distinct to separate it from *S. cornuta* on morphological grounds.

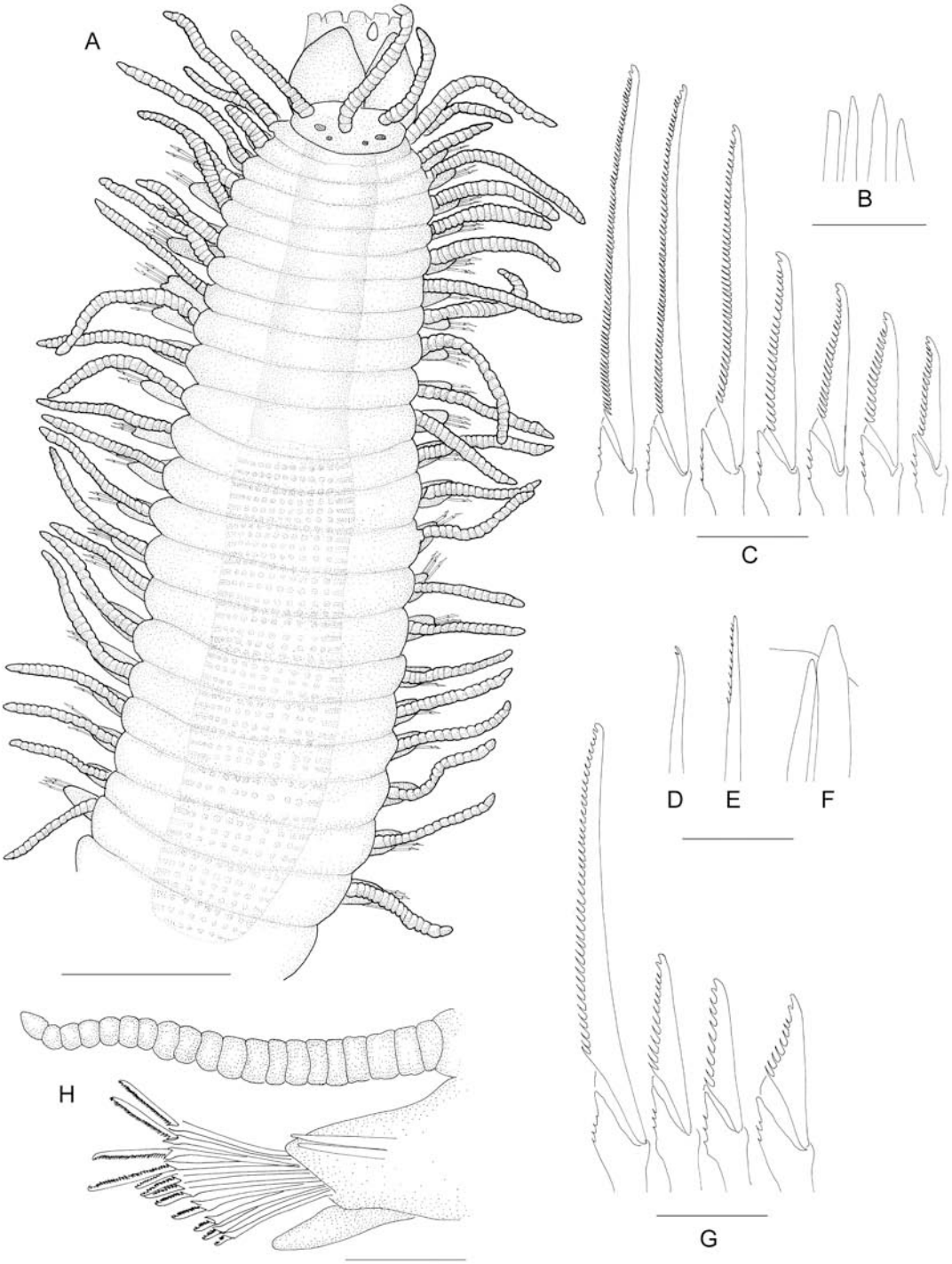

Figure 9. *Syllis* cf. *cornuta* ZMA V. Pol. 2211.02. A: Anterior part, dorsal view; B: Anterior aciculae; C: Anterior chaetae; D: Ventral simple chaeta; E: dorsal simple chaeta; F: Posterior aciculae; G: Posterior chaetae; H: Midbody parapodium, anterior view. Scale A: 0.5 mm; B-G: 20 µm; H: 0.2 mm.

Distribution. Indonesia. The nominal species occurs in: North Sea, North West Atlantic Ocean, Bering Sea, Pacific Ocean (North West, Japan (?) and Eastern Australia (?)), Mediterranean Sea (?), Red Sea (?), Indian Ocean (South Africa (?)) (? *fide* Licher, 1999).

Syllis cf. _cruzi_ Núñez & San Martín, 1991

Fig. 10

Material examined. 1 spec. ZMA V.Pol. 5262, Indonesia, Komodo, NE cape, 08°29'S 119°34.1'E, sandy bottom, algae, occasional sponges and tunicates, 30-34 m, Snellius II, Sta. 4.096d, 19/20 Sept. 1984.

Comparative material examined.

Syllis cruzi Núñez & San Martín, 1991. Several spec. MNCN16.01/6744, Spain, Castellón, Is. Columbretes, N de Columbreta Grande, 39°54' 02"N 00°41'15"E, 47 m, 12 July 1994; several spec. MNCN 16.01/6745, Spain, Is. Baleares, Mallorca, Punta de la Foradada, 39º44'33"/39º45' 80"N 02º31' 86"/02º33' 51"E, 72-74 m, 25 Jun. 1994 (all identified by San Martín, 2003).

Syllis curticirris (Hartmann-Schröder, 1981). Holotype ZMH P16462 and paratype ZMH P16463, Central Atlantic Ocean, Meteor Bank, 29º58.6'N 28º25.1'W, 300-330 m.

Description. Specimen 15 mm long, 0.5 mm wide, with 117 segments. Distinct glandular bands in lateral and posterior margins of each segment (Fig. 10A). Prostomium wider than long, with two pairs of eyes in trapezoidal arrangement, anterior ones larger than posterior pair, eyespots absent. Median antenna inserted on middle of prostomium, between anterior pair of eyes, slightly longer than combined length of prostomium and palps, with 18 articles. Shorter lateral antennae inserted on anterior margin of prostomium, with 13 articles. Palps broad, triangular, longer than prostomium, fused at base, with median groove. Peristomium shorter than subsequent segments (Fig. 10A). Dorsal tentacular cirri equal in length to median antenna, with 18 articles, ventral ones shorter, with 11 articles. Anterior-most dorsal cirri longer than subsequent ones, with 16-19 articles; from chaetiger 4 backwards, dorsal cirri shorter, with 12-13 articles. Posterior dorsal cirri short, with 7-10 articles. Ventral cirri digitiform, proximally inserted, shorter than parapodia. Anterior parapodia each with

13-14 compound, heterogomph chaetae. Bidentate blades (ca. 23-26 μm) with two to three distal spines on blade edge longer than basal ones (Fig. 10B). Posterior chaetigers with 12 bidentate compound chaetae, shorter and thicker than those of anterior chaetigers (most dorsal ca. 23 μm, most ventral ca. 16 μm), with spines on blade edge; two to three most distal spines much longer than others, reaching to level of proximal tooth (Fig. 10F). One unidentate, dorsal simple chaeta with short distal spines (Fig. 10D). One bidentate ventral simple chaeta in posterior parapodia, with three long spines on tip (Fig. 10E). Anterior parapodia with three aciculae, two pointed and other distally curving (Fig. 10C); posterior parapodia with one acicula distally curving (Fig. 10G). Pygidium regenerating, two anal cirri with 10-11 articles. Pharynx equal in length to proventricle, through eight segments; conical tooth on anterior margin. Proventricle with about 31 cell-rows with distinct longitudinal midline (Fig. 10A).

Remarks. Syllis cruzi has been reported from the Atlantic Ocean (Canary Islands) (Núñez & San Martín, 1991) and Western Mediterranean Sea (San Martín, 2003), geographical areas far from Indonesia. However, we did not find any clear difference between the single specimen described above and the Mediterranean material. Some small variations have been found between the holotype and our specimen, e. g. dorsal cirri of holotype are slightly shorter in the anterior part, alternating in length (eight to nine articles the longest, and six to seven the shortest), while they are 12-13 in *S.* cf. *cruzi* and a pattern of alternating lengths has not been seen. The specimen from Indonesia is much longer (15 mm) than the holotype (5 mm). Examined specimens from the Mediterranean, which are longer (9 mm), have more articles in the dorsal cirri and in this respect more closely resemble the Indonesian specimen (10-12 the shortest and 16-18 the longest). It appears that the number of articles present on the dorsal cirri is related to body length; however, the alternation in length of dorsal cirri in the holotype could be a difference. *Syllis* cf. *cruzi* shows distinctive glands in the lateral and posterior margins of each segment, a character that was not described for the type material, not for any of the Mediterranean specimens of *S. cruzi* (Núñez & San Martín, 1991; San Martín, 2003). However, we do not consider the presence of glands to be a useful diagnostic character; it might, for instance, appear only during the reproductive stage (San Martín, 2003). More specimens would be needed to establish if the presence of glands and dorsal cirri, not alternating in length, are consistent characters and if so this could be useful to distinguish species within this group.

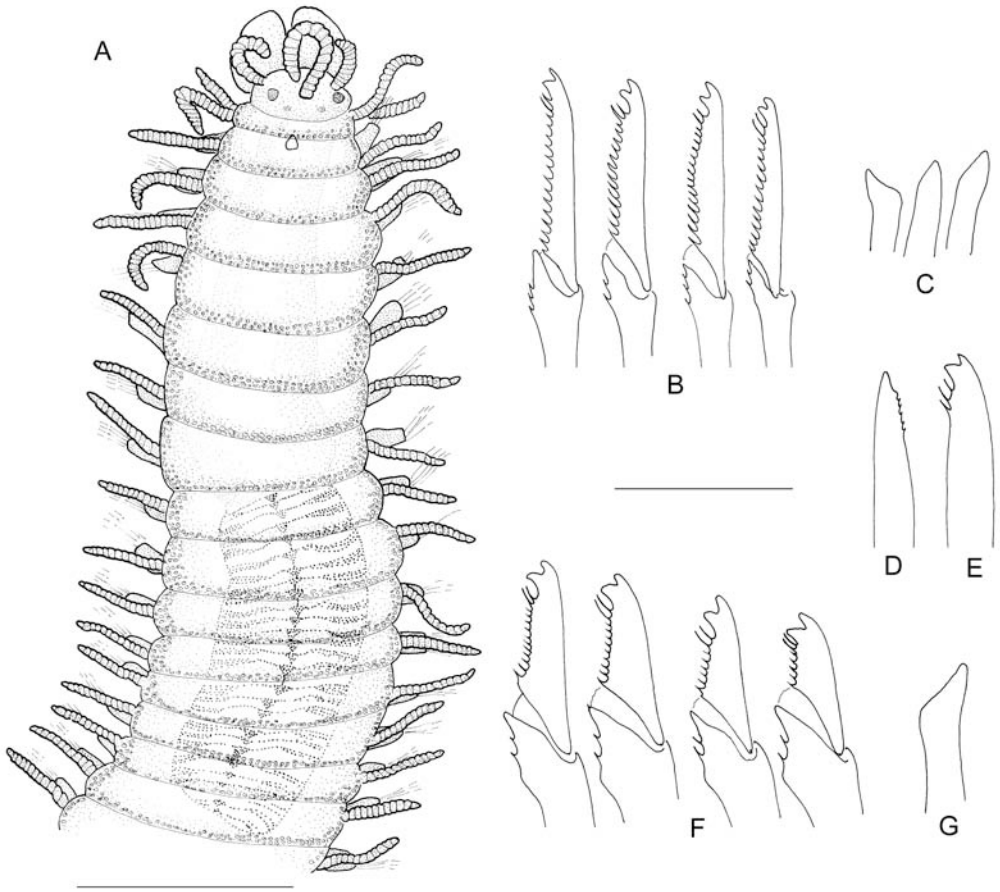

Figure 10. *Syllis* cf. *cruzi* ZMA V. Pol. 5262. A: Anterior part, dorsal view; B: Anterior chaetae; C: Anterior aciculae; D: Dorsal simple chaeta; E: Ventral simple chaeta; F: Posterior chaetae; G: Posterior acicula. Scale A: 0.5 m; B-G: 20 µm.

Other species sharing a similar chaetal shape are *Syllis lutea* Hartmann-Schröder, 1960 (circumtropical), *S. curticirris* Hartmann-Schröder, 1981 (Atlantic Ocean) and *Dentatisyllis carolinae* (Day, 1973) (Atlantic Ocean). *Syllis lutea* differs in having several longer distal spines on the edge of the blade (Hartmann-Schröder, 1960; Licher, 1999) while *S.* cf. *cruzi* only has one or two. *Syllis curticirris* has short dorsal cirri, with only three articles (Licher, 1999; this study), while there are about 12-13 in *S.* cf. *cruzi*. *Dentatisyllis carolinae* has a trepan opening and the dorsal simple chaetae are distinctly bidentate (Day, 1973; Uebelacker, 1984), whereas *S.* cf. *cruzi* has a smooth anterior margin and unidentate simple dorsal chaetae. Chaetae of *Syllis gerundensis* (Alós & Campoy, 1981) (Mediterranean Sea) are also similar in shape, but spines on the edge of the blade are all short. In addition, dorsal cirri of this species are shorter, with five to seven articles on midbody (Alós & Campoy, 1981; Licher, 1999). *Syllis*

glandulata Nogueira & San Martín, 2002 (Brazil) has similar glands on the lateral sides of each segment, but the spines of the compound chaetae are short (Nogueira & San Martín, 2002).

Distribution. Indonesia. The nominal species occurs in the Atlantic Ocean (Canary Islands) and Western Mediterranean Sea.

***Syllis komodoensis* n. sp.**

Figs 11-13

Material examined. Holotype ZMA V.Pol. 5263 and 4 paratypes (one mounted for SEM) ZMA V.Pol. 5264, Indonesia, Komodo, NE cape, 08°29'S 119°34.1'E, edge of narrow coastal reef, sloping down to sandy bottom with algae, occasional sponges and tunicates, 30-34 m, Snellius II, Sta. 4.096d, 19/20 Sept. 1984.

Comparative material examined.

Syllis hyalina Grube, 1863. 1 syntype MPW 396, Adriatic Sea, Croatia, Lussin (= Losinj).

Syllis armillaris. Several spec. MNCN 16.01/7906-07, Spain, Almería, Cabo de Gata, 2 m, 36º46’49.11’’N 2º14’25.31’’W, Jan. 1987. (Identified by San Martín, 2003).

Description. Holotype 12.2 mm long, 0.4 mm wide, with 93 segments; paratypes 15 mm, 7.5 mm and 6 mm long, 0.4 mm wide, with 109, 72 and 62 segments respectively. Prostomium wider than long, with two pairs of eyes in trapezoidal arrangement, anterior ones larger than posterior pair, eye spots absent (Fig. 11A). Median antenna inserted on middle of prostomium (Figs 11A, 13A, B), slightly longer than combined length of prostomium and palps, with 16 articles; lateral antennae shorter, inserted on anterior margin of prostomium, with 10-12 articles. Palps triangular, longer than prostomium, fused at base, with distinct median groove. Nuchal organs forming ciliary groove between prostomium and peristomium (Fig. 13B). Peristomium similar in length to subsequent segments. Two pairs of tentacular cirri: dorsal ones longer than antennae, with 25 articles, ventral ones shorter, with 11 articles. Dorsal cirri of most anterior segments with 17-22 articles. From segment four towards posterior end dorsal cirri shorter, alternating in length, shortest with nine, longest with 13 articles. Basal articles narrower than distal ones, increasing in width and length in middle of cirri, becoming

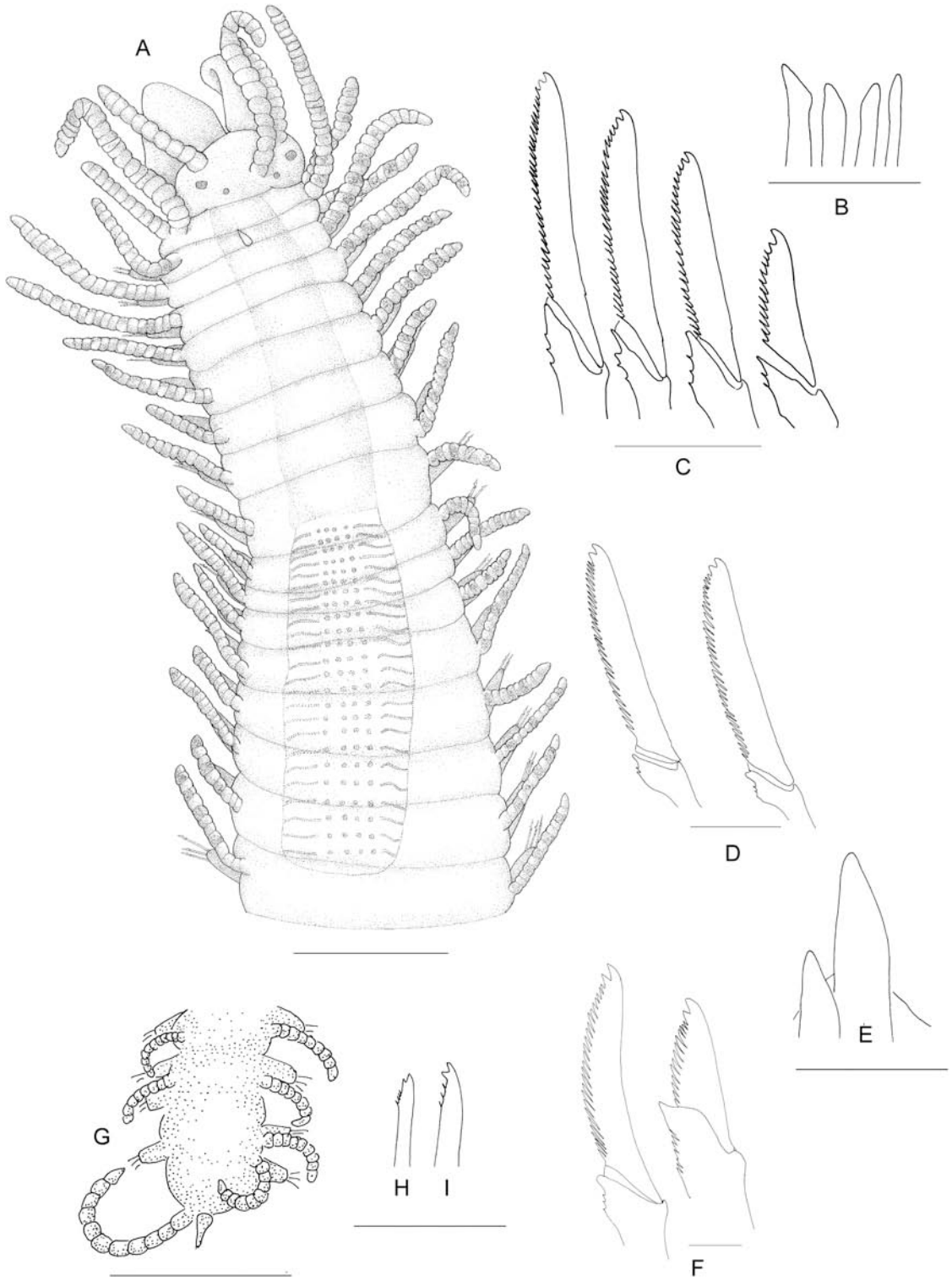

Figure 11. *Syllis komodoensis* n. sp. A: Anterior part, dorsal view, holotype ZMA V. Pol. 5263; B: Anterior aciculae, holotype ZMA V. Pol. 5263; C: Anterior chaetae, holotype ZMA V. Pol. 5263; D: Midbody chaetae, holotype ZMA V. Pol. 5263; E: Midbody aciculae, holotype ZMA V. Pol. 5263; F: Posterior chaetae, holotype ZMA V. Pol. 5263; G: Posterior part, dorsal view, paratype ZMA V. Pol. 5263; H: Dorsal simple chaeta, holotype ZMA V. Pol. 5263; I: Ventral simple chaeta, holotype ZMA V. Pol. 5263. Scale A, G: 0.2 mm; B-C: 20 µm; D: 10µm; E, H-I: 20 µm; F: 5 µm.

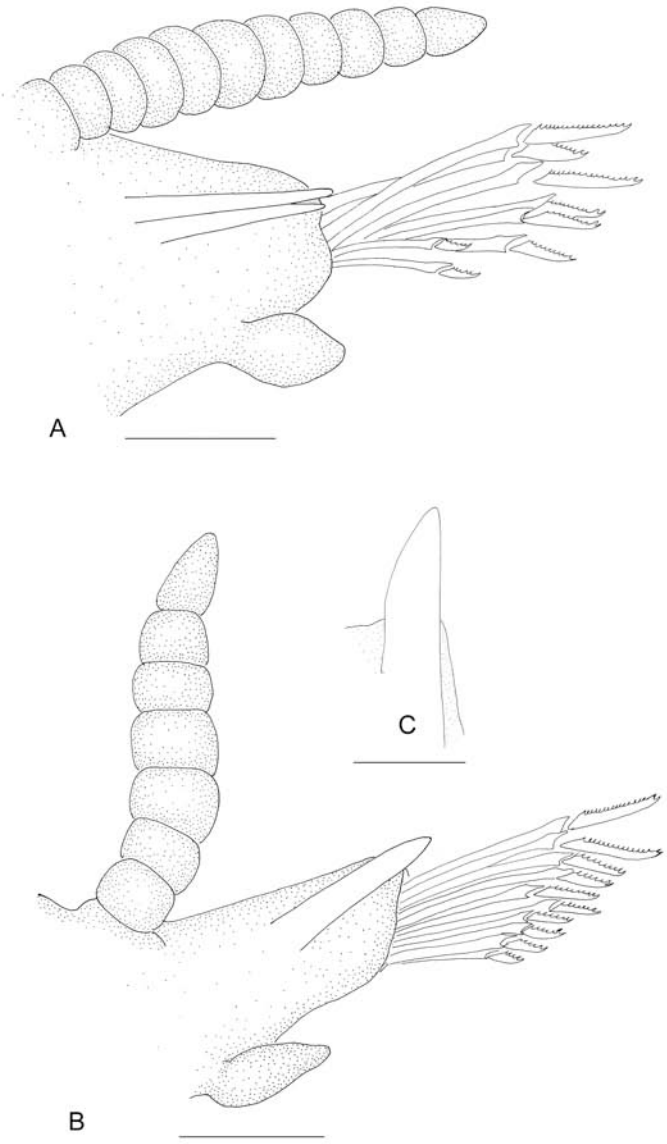

Figure 12. *Syllis komodoensis* n. sp. Holotype ZMA V. Pol. 5263. A: Midbody parapodium, anterior view; B: Posterior parapodium, anterior view; C: Posterior acicula. Scale A, B: 48 µm; C: 20 µm.

short and narrow again distally (Figs 12A, B). Spiral glands inside articles. Anterior ventral cirri digitiform, inserted proximally and reaching distal end of parapodia (Fig. 12A). Ventral cirri becoming shorter from midbody (after the proventricle) to posterior end, being pear- shaped on posterior parapodia (Fig. 12B). Anterior parapodia each with nine compound, heterogomph chaetae. Long bidentate blades, dorsoventrally decreasing in length (ca. 40 µm dorsal-most, ca. 20 µm ventral-most), short spines on edge (Figs 11C, 13C, E). Midbody parapodia with nine compound chaetae, bidentate blades similar

in length to anterior ones, longer spines on edge (Figs 11D, 13F). Posterior parapodia with 11 compound chaetae, blades bidentate, shorter than those of anterior parapodia (dorsal-most ca. 30 μm, ventral-most ca. 16 μm), spines on edge (Figs 11F, 13G, H). Dorsal simple chaetae on posterior parapodia, distinctly bidentate, with short subdistal spines on edge (Fig. 11H). Ventral simple chaetae on posterior parapodia, bidentate with short spines on edge (Fig. 11I). Anterior parapodia with three to four pointed aciculae, distally curving (Figs 11B, 13D, E); midbody with two pointed aciculae protruding from each parapodial lobe (Figs 11E, 12A); posterior segments with a single huge, straight and protruding acicula (Figs 12B, C). Pygidium conical with two short anal cirri (three articles, 11 in one paratype) and one medial anal papilla (only visible in one paratype) (Fig. 11G). Pharynx similar in length to proventricle, through nine segments; conical tooth on anterior margin. Proventricle extending through eight segments, with about 24 rows of muscular cells (Fig. 11A).

Remarks. *Syllis komodoensis* n. sp., is characterized by short dorsal cirri (shorter than body width), long bidentate blades on midbody to posterior chaetigers and one large acicula distinctly protruding from parapodial lobes on posterior parapodia. *Syllis komodoensis* n. sp. shares some characters with other species of *Syllis* but this combination of characters is not present in any other described species. Several species have similar dorsal cirri but differ in other characters. In *S. hyalina*, *S. armillaris* (both regarded as a cosmopolitan species) and *S. pseudoarmillaris* Nogueira & San Martín, 2002 (Atlantic Ocean), blades' length of midbody to posterior chaetae and their spines are shorter, and the posterior aciculae are much smaller (Nogueira & San Martín, 2002). *Syllis mayeri* Musco & Giangrande, 2005 (Caribbean) has unidentate posterior compound chaetae, tending to an "ypsiloid" condition (Musco & Giangrande, 2005) (the term "ypsiloid" is used to describe a thick Y-shaped chaeta produced by total or partial fusion of shaft and blade). *Syllis gracilis* Grube, 1840 (regarded as a cosmopolitan species) and *S. magellanica* Augener, 1918 (Pacific and Indian Ocean) possess ypsiloid chaetae (Grube, 1840; Augener, 1918; Licher, 1999; San Martín, 2003). Another important character, shared with a different group of taxa, is the presence of one large acicula emerging from the posterior parapodia; but, *Syllis aciculata* Treadwell, 1945 (Pacific Ocean, China Sea) has long dorsal cirri (longer than body width, about 20-24 articles in midbody chaetigers) and parapodia with pre- and postchaetal lobes (Treadwell, 1945; Licher, 1999). *Syllis variegata* Grube, 1860

(regarded as a cosmopolitan species) has shorter blades in its compound chaetae, with short and thick spines and a characteristic colour pattern (Grube, 1860; Licher, 1999).

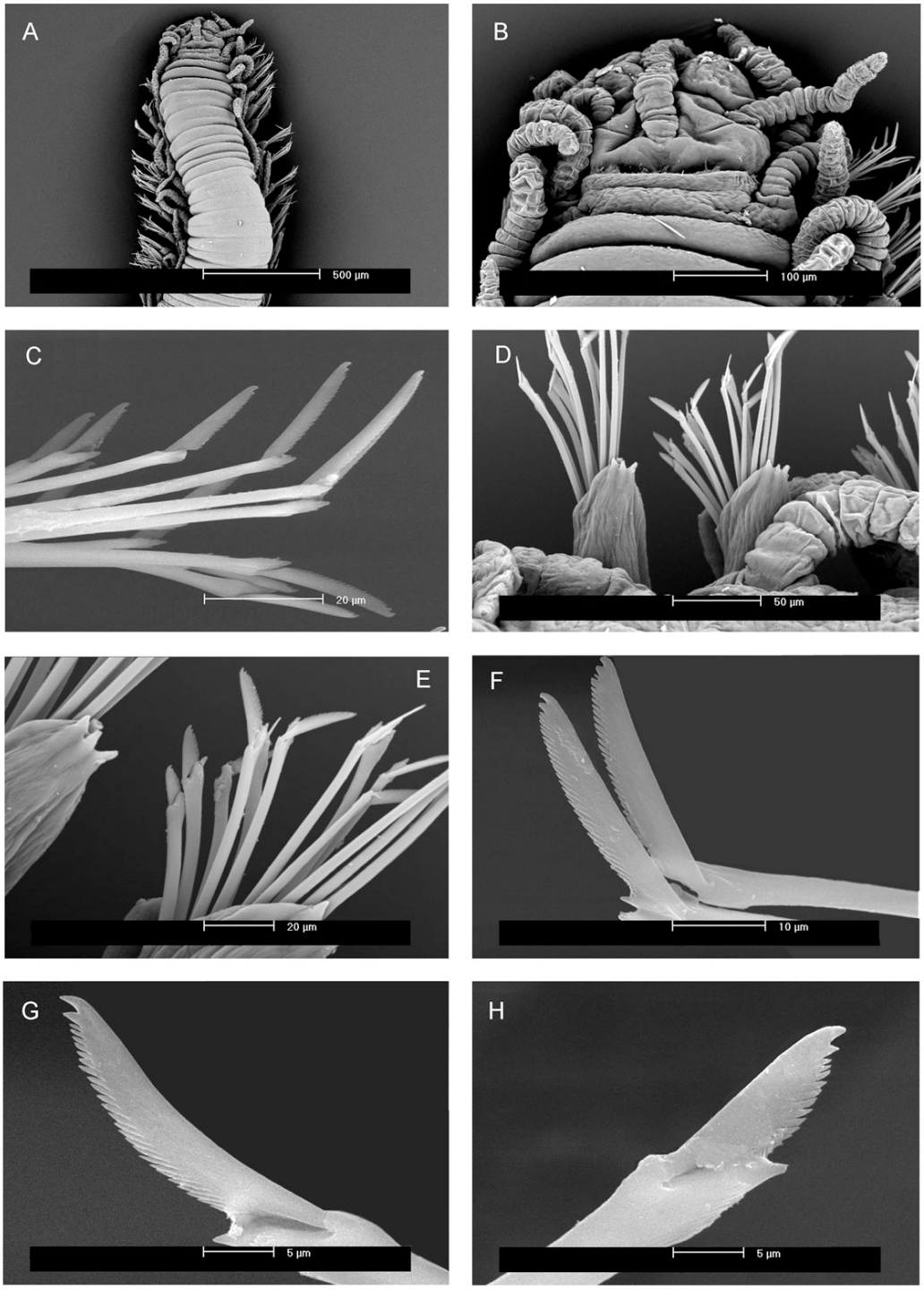

Figure 13. *Syllis komodoensis* n. sp. Paratype ZMA V. Pol. 5264. SEM. A: Anterior part, dorsal view; B: Prostomium, dorsal view; C: Anterior chaetae; D: Anterior parapodia, dorsal view; E: Anterior midbody parapodia, dorsal view; F: Midbody chaetae; G: Posterior chaeta; H: Posterior chaeta.

Finally, *Syllis crassicirrata* Hartmann-Schröder, 1979 (Pacific and Indian Ocean) has compound chaetae with much shorter blades and very long dorsal cirri (40 articles) (Hartmann-Schröder, 1979; Licher, 1999). Length and shape of blades are similar to those present in *Syllis gerlachi* (Hartmann-Schröder, 1960) (Red Sea, Mediterranean Sea, Caribbean and Indian Ocean). However, this taxon has a truncate posterior acicula and one thick and truncate simple dorsal chaeta (San Martín, 2003).

Distribution. Indonesia.

Etymology. The specific name refers to the type-locality, the island of Komodo.

***Syllis lutea* (Hartmann-Schröder, 1960)**

Typosyllis lutea Hartmann-Schröder, 1960: 81, pl.2, fig. 38, pl. 5, figs 39-41. - Hartman, 1974: 617. - Licher, 1999: 177, 178, fig. 79.

Typosyllis (Typosyllis) lutea. - Hartmann-Schröder, 1979: 89-90; 1980: 389-390; 1981: 27; 1982: 59; 1991: 29; 1992: 56-57.

Material examined. 1 spec. ZMA V.Pol. 2046 (as *Syllis zonata*), Philippines, Sulu Archipelago, anchorage off Pulu Tongkil, dredge, lithothamnion bottom, 13m, Siboga Expedition, Sta. 109, 5/6 July 1899.

Remarks. The specimen agrees well with the descriptions.

Distribution. Circum(sub)tropical.

***Syllis* cf. *parapari* San Martín & López, 2000**

Fig. 14

Material examined. 1 spec. ZMA V.Pol. 1998 (as *Syllis cerina*), Indonesia, Sulawesi, Buton Strait, Lohio Bay, dredge, townet, muddy bottom, 22 m, Siboga Expedition, Sta. 205, 20 Sept. 1899.

Comparative material examined

Syllis parapari Holotype MNCN 16.01/6070, Spain, ría de El Ferrol, gravel, sublittoral, 43º27´1´´N 8º19´16´´W, 2 Jun. 1987, on permanent microscope slide; Paratypes MNCN

16.01/6071, Spain, ría de El Ferrol, muddy sand, 21 m, 43º27.49´´N 8º16.42´´W, 5 Aug. 1987, two spec. on permanent microscope slides; MNCN 16.01/6072, Spain, ría de El Ferrol, muddy sand, 15 m, 43º27´26´´N 8º20´06´´W, 6 Jul. 1987, one spec. on permanent microscope slide; MNCN 6.01/6074, Spain, off ría de Muros, muddy sand with shells, 85 m, 42º41.6´N 9º10.3´W, 11 Jun. 1991; MNCN 16.01/6075, Spain, off Cabo Finisterre, rocky botton, 129-133 m, 42º51.89´N 9º21.19´W, 11 jun. 1991; MNCN 16.01/6076, Spain, NW Sisargas Is., black mud, 157-159 m, 43º26´N 8º59.35´W, 12 Jun. 1991; MNCN 16.01/6077, Spain, off Girón, biocenosis of *Dendrophyllia ramea*, 116-120 m, 43º43,71´N 5º56.21´W, 15 Jun. 1991; MNCN 16.01/6078, Spain, off San Sebastián, mud, 135-143 m, 43º29.72´N 2º0.89´W, 22 Jun. 1991.

Description. Specimen 11.6 mm long, 0.8 mm wide, with 101 segments. Body strongly pigmented red. Prostomium wider than long, with two pairs of eyes in trapezoidal arrangement, posterior ones larger than anterior pair, eye spots absent. Median antenna inserted on middle of prostomium, between anterior pair of eyes, longer than combined length of prostomium and palps, with 25 articles; shorter lateral antennae inserted at anterior margin of prostomium, with 15-18 articles. Palps triangular, longer than prostomium. Peristomium similar in length to subsequent segments (Fig. 14A). Dorsal tentacular cirri similar in length to median antenna, with 15 articles, ventral ones shorter with 13 articles. Articles of dorsal cirri basally broad, distally tapering. Anterior dorsal cirri with 14-15 articles, some of them shorter with 10-11 articles. Midbody and posterior dorsal cirri all short, with 8-10 articles. Cirrophores present. Anterior ventral cirri digitiform, inserted proximally and exceeding length of parapodia. Posteriorly, ventral cirri becoming shorter, not extending beyond parapodia. Anterior parapodia each with eight to nine bidentate, compound, heterogomph chaetae, two pseudospiniger blades (ca. 75 µm), remaining falcigers (ca. 28-30 µm), both groups with spines on blade edge (Fig. 14C). Midbody chaetigers with two pseudospinigers shorter than anterior ones (ca. 60 µm) and eight falcigers (ca. 25-30 µm) (Fig. 14D). Posterior chaetigers with one or two shorter pseudospinigers (ca. 50 µm), and six to seven falcigers (ca. 20-24 µm) (Fig. 14F). Simple dorsal chaetae unidentate, with short subdistal spines on edge and single ventral chaeta, bidentate, with small proximal tooth and short spines on edge, both on posterior parapodia. Anterior parapodia with four to six pointed and acuminate aciculae (Fig. 14B) gradually decreasing in number to one or two posteriorly (Fig. 14E). Pygidium regenerating, anal cirri absent. Pharynx extending

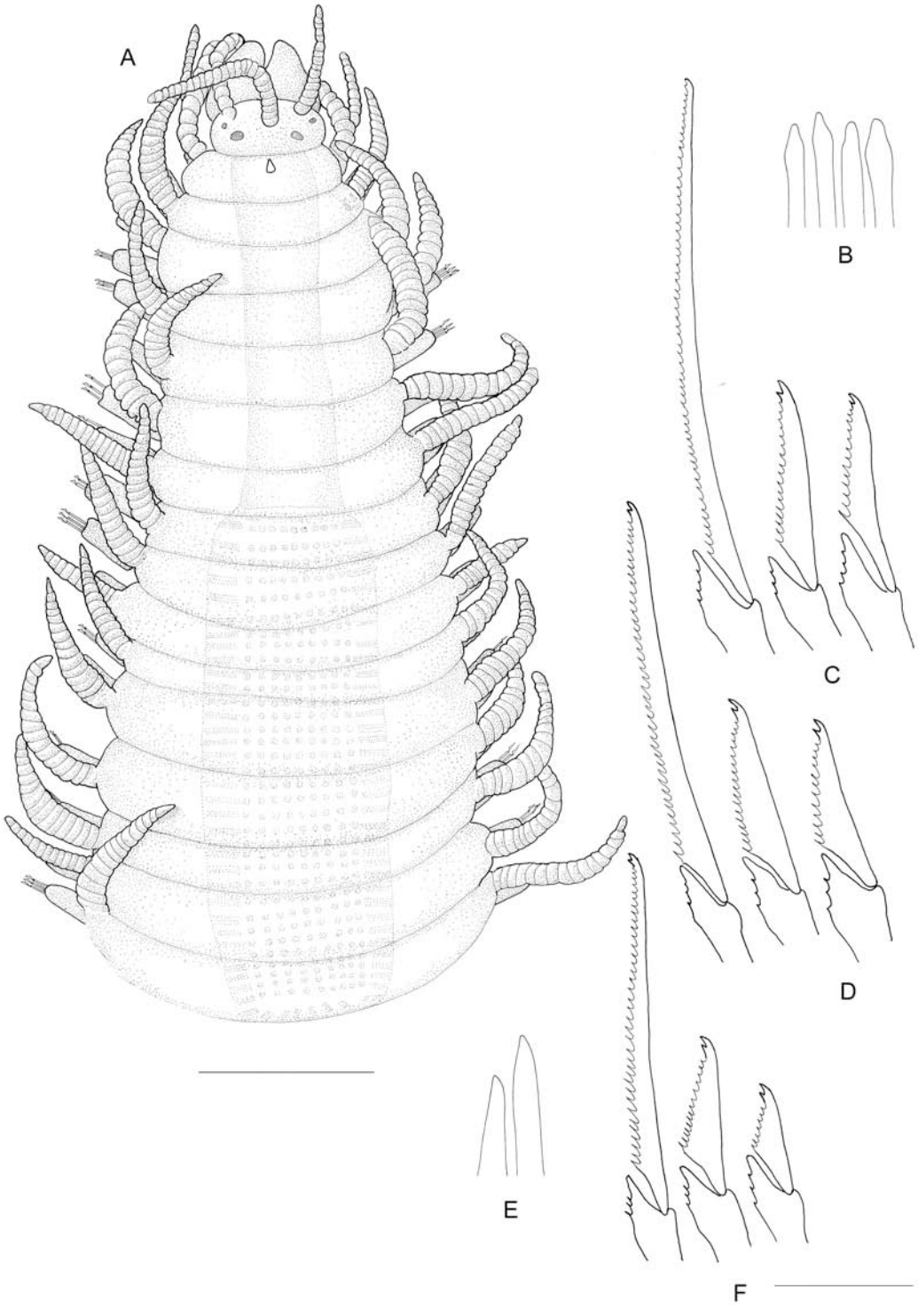

Figure 14. *Syllis* cf. *parapari* ZMA V. Pol. 1958. A: Anterior part, dorsal view; B: Anterior aciculae; C: Anterior chaetae; D: Midbody chaetae; E: Posterior aciculae; F: Posterior chaetae. Scale A: 0.4 mm; B-F: 20 µm.

through seven segments; conical tooth located on anterior margin. Proventricle through nine segments, cell-rows difficult to ascertain (Fig. 14A).*Remarks.* Some specimens from the Iberian coasts of the Atlantic Ocean, originally identified as *S. cornuta* by Campoy (1982) and Parapar *et al.* (1996), were re-described by San Martín & López (2000) as *S. parapari* because they were clearly different with regards to the shape of aciculae and shape and length of dorsal cirri. The specimen from Indonesia agrees with the description and type series of *S. parapari*. Although re-examination of the presumedly worldwide *S. cornuta* might reveal misidentified populations of *S. parapari* between Spain and Indonesia, we prefer to maintain our doubt on the identity of our single Indonesian specimen.

Distribution. Indonesia. The nominal species occurs in the Atlantic Ocean (Spain).

***Syllis setoensis* (Imajima, 1966) n. comb.**

Typosyllis setoensis Imajima, 1966: 284-286, figs 62 a-l. - Licher, 1999: 124, 125, fig. 56.

Material examined. 1 spec. ZMA V.Pol. 1986.03 (as *Syllis brachychaeta*), Indonesia, anchorage off the south point of Kabaëna Isl., 22 m, Siboga Expedition, Sta. 209, 23 Sept 1899.

Remarks. In agreement with San Martín (1984, 1992, 2003), the genus *Typosyllis* is not accepted herein, thus *Syllis setoensis* is a new combination. The specimen agrees well with the original description.

Distribution. Pacific (Japan), Indonesia.

***Syllis variegata* Grube, 1860**

Syllis variegata Grube, 1860: 85, 86. - San Martín, 2003: 351-354, figs 190, 191.
Typosyllis variegata - Licher, 1999: 101-108, fig. 49.

Material examined. 1 spec. ZMA V.Pol. 2019.03 (as *Syllis variegata*), Indonesia, Sulawesi, Binongka, W coast, anchorage off Pasir Pandjang, townet, dredge, coral sand, 278 m, Siboga Expedition, Sta. 220, 1/3 Nov. 1899; 1 spec. ZMA V.Pol. 2042 (as *Syllis*

variegata), Indonesia, Paternoster Isl., Sailus Ketjil, dredge, coral and coral sand, up to 27 m, Siboga Expedition, Sta. 37, 30/31 March 1899; 1 spec. ZMA V.Pol. 1986.03 (as *Syllis brachychaeta*), Indonesia, anchorage North of Salomakiëe (Damar-) Isl., dredge, townet, reef exploration, corals, down to 45 m, Siboga Expedition, Sta. 144, 7/9 Aug. 1899; 1 spec. ZMA V.Pol. 2227.02 (as *Syllis brachychaeta*), Indonesia, Paternóster Isl., Sailus Ketjil, dredge, coral and coral sand, down to 27 m, Siboga Expedition, Sta. 37, 30/31 March 1899.

Remarks. Except for the typical colour pattern, the specimens agree well with the previous descriptions. However, more than 100 years in alcohol may have caused the loss of pigmentation.

Distribution. Apparently cosmopolitan in warm seas.

***Syllis villenai* n. sp.**
Fig. 15

Material examined. Holotype ZMA V.Pol. 1985.01 (as *Syllis exilis*), Indonesia, 5º56.7´N 126º25´E, 0-36 m, Siboga Expedition, Sta. 133, 25/27 July 1899.

Description. Specimen 40 mm long, 1 mm wide, with 192 segments. Body strongly pigmented red. Prostomium wider than long, with two pairs of eyes in trapezoidal arrangement. Median antenna arising from middle of prostomium, long, with 42 articles, reaching to segment 10; lateral antennae inserted at anterior margin of prostomium, shorter than median one, slightly longer than combined length of prostomium and palps, with 22-28 articles. Palps broad, slightly longer than prostomium, fused at base, with a distinct median groove (Fig. 15A). Peristomium similar in length to subsequent segments, with two pairs of tentacular cirri. Dorsal tentacular cirri with 43 articles, ventral ones shorter with 22-24 articles. Anterior and midbody parapodia longer than posterior ones. Pre- and postchaetal lobes present on all parapodia, both similar in length (Fig. 15G). Dorsal cirri long (Fig. 15A) inserted far above parapodia, with spiral inclusions within all articles (Fig. 15G). Dorsal cirri alternating in length in anterior and middle part of body (Fig. 15A), longer ones with 50-80, shorter with 30-40 articles. In posterior part longer cirri with 40-50 articles,

shorter with 15. Distinct cirrophores present on all segments. Ventral cirri digitiform, not extending beyond parapodial lobes, inserted on middle of parapodia on anterior and midbody parapodia (Fig. 15G), becoming more proximally inserted posteriorly. Distinct dark parapodial glands present from segment 22 onwards (Fig. 15G). Anterior parapodia each with 12 compound, heterogomph chaetae; distal part of shafts provided with spines, bidentate blades (ca. 40 µm dorsalmost, 35 µm ventral most), both teeth similar in size and length; edge with long spines, longer than distal tooth (Fig. 15B). Midbody and posterior chaetigers with 8-12 compound heterogomph chaetae, dorsoventrally decreasing in length (ca. 35 µm dorsal-most, ca. 30 µm ventral-most), proximal tooth slightly bigger than distal one, both robust. Most ventral blades on posterior parapodia with four to five long and thin spines on margin, not exceeding distal tooth in length (Fig. 15C). Dorsal and ventral simple chaetae not seen. Three straight aciculae per parapodium (Figs 15D, E). Pygidium conical, with two long articulated anal cirri, with 27-28 articles (Fig. 15F). Pharynx long, extending through 14 segments, with pharyngeal tooth on anterior margin, crowned by ten triangular papillae. Proventricle long, extending through 15 segments, cell-rows difficult to distinguish (Fig. 15A).

Remarks. Syllis villenai n. sp., is characterized by having long dorsal cirri which alternate in length (30-80 articles in midbody chaetigers), bidentate compound chaetae with long spines on edge of blade, with thick and rounded distal teeth on posterior parapodia; long pharynx and proventricle and dark parapodial glands in midbody to posterior chaetigers. The similar *Syllis lutea* (originally described from the Red Sea) also has bidentate compound chaetae with long spinulation and distal thicker teeth in the posterior part of the body. However, in anterior and midbody parapodia of *S.lutea* long spines are only present on the most ventral chaetae, the most dorsal ones have shorter spines. In posterior parapodia, basal spines remain short and only in the distal edge of the blade, do spines become as long as the distal teeth (Hartmann-Schröder, 1960, Licher, 1999). *Syllis glarearia* Westheide, 1974 (Pacific Ocean) is also similar in having long spines and thick distal teeth, but the anterior blades are considerably shorter and there are only two or three long spines on the distal part of the edge (Westheide, 1974, Licher, 1999). *Syllis bifurcata* Hartmann-Schröder, 1980 (Indian Ocean and Caribbean) also has posterior bidentate compound chaetae with enlarged distal teeth, but it differs in the length of dorsal cirri (22-27 articles in midbody chaetigers), with blades with

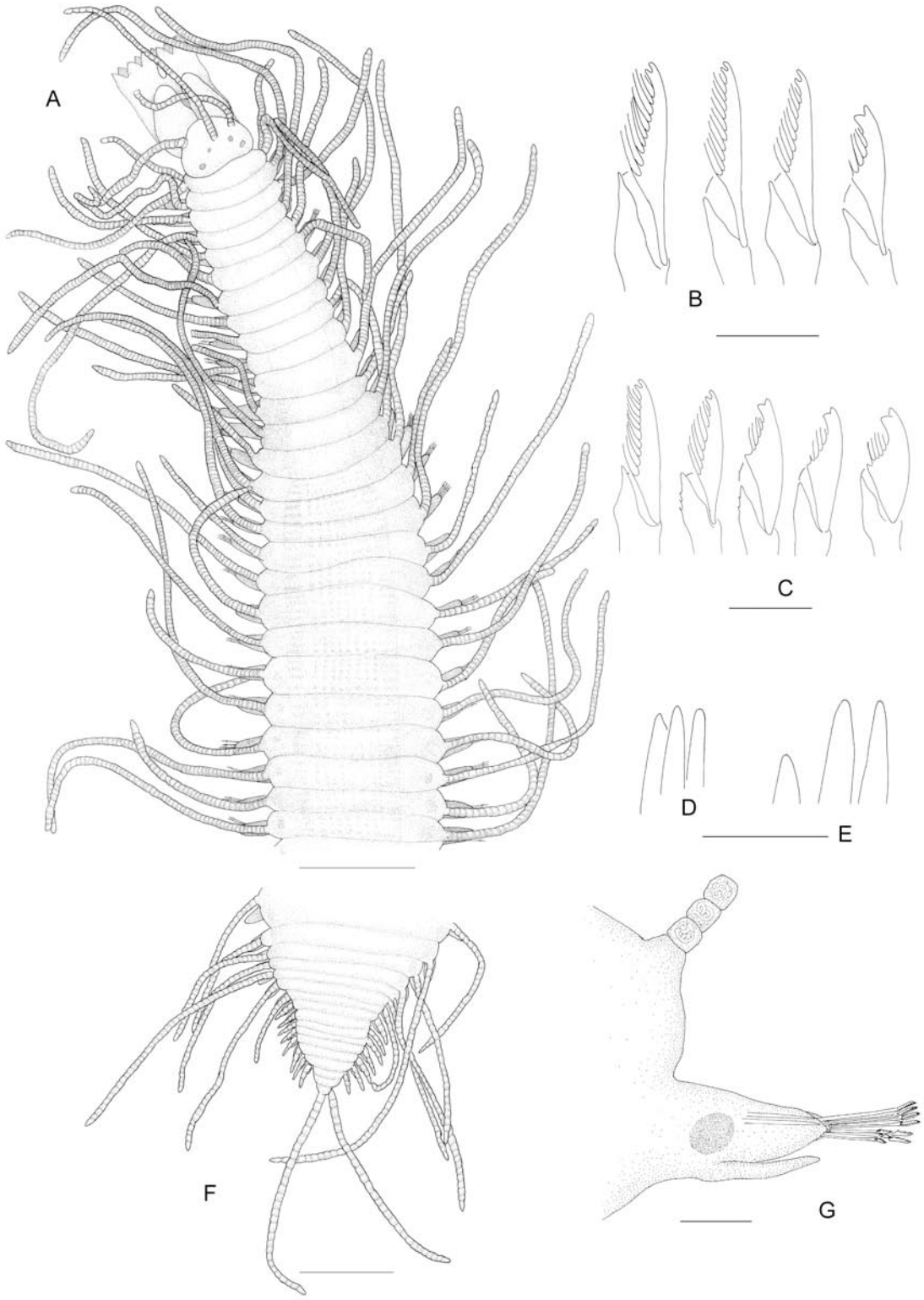

Figure 15. *Syllis villenai* n. sp. Holotype ZMA V. Pol. 1985.01. A: Anterior part, dorsal view; B: Anterior chaetae; C: Posterior chaetae; D: Anterior aciculae; E: Posterior aciculae; F: Posterior part, dorsal view; G: Midbody parapodium, anterior view. Scale A, F: 0.5 mm; B-E: 20 µm; G: 48 µm.

shorter spines and fangs with two distal tips, one of them extremely large on posterior chaetae (Hartmann-Schröder, 1980; Licher, 1999). Although there is only one specimen, we believe that is so distinctive to be described as a new species.*Distribution*. Indonesia.

Etymology. This species is dedicated to Miguel Villena, the curator Invertebrates of the MNCN, who has assisted and help us in several studies with loan and deposition of material.

***Syllis ypsiloides* n. sp.**
Figs 16-18

Material examined. Holotype ZMA V.Pol. 5265, Indonesia, Teluk Ambon, near Tawiri, 03°42'S 128°07'E, sandy bottom with *Acropora* and sponges, 1-5 m, Snellius II, Sta. 4.010, 6 Sept. 1984; paratype (mounted for SEM) ZMA V.Pol. 5266, Indonesia, NE coast of Sumba, 09°57'S 120°48'E, sandy bottom, sponges and gorgonians, 50 m, 1.2 m Agassiz trawl, Snellius II, Sta. 4.068, 16 Sept. 1984; 2 Paratypes ZMA V.Pol. 1988.01, 1988.02 (as *Syllis gracilis*), Indonesia, Lesser Sunda Isl., Bay of Bima, near south fort, trawl, dredge, muddy bottom with coral sand, 55 m, Siboga Expedition, Sta. 47, 8/12 April 1899.
Comparative material examined.
Syllis gracilis. 1 syntype MPW395, Mediterranean Sea, Adriatic Sea; several spec. MNCN 16.01/ 8927, 8928, 8936, 8938, 8948, Spain, Málaga, Nerja, 36º44’28.85’’N 3º52’47.15’’W, Dec. 1982-Aug. 1983. (identified by San Martín, 2003).

Description. Holotype incomplete 17 mm long, 0.5 mm wide, with 113 segments; best preserved paratype incomplete 43 mm long, 0.3 mm wide, with 56 segments. Prostomium wider than long, with two pairs of eyes in trapezoidal arrangement, anterior ones larger than posterior pair. Median antenna with 17 articles, inserted on middle of prostomium, slightly longer than combined length of prostomium and palps; shorter lateral antennae with 11 articles, inserted on anterior margin of prostomium. Palps triangular, similar in length to prostomium (Figs 16A, 17A, B), fused at base, with distinct median groove. Peristomium shorter than subsequent segments, with two pairs of tentacular cirri. Nuchal organs not seen. Dorsal tentacular cirri longer than lateral

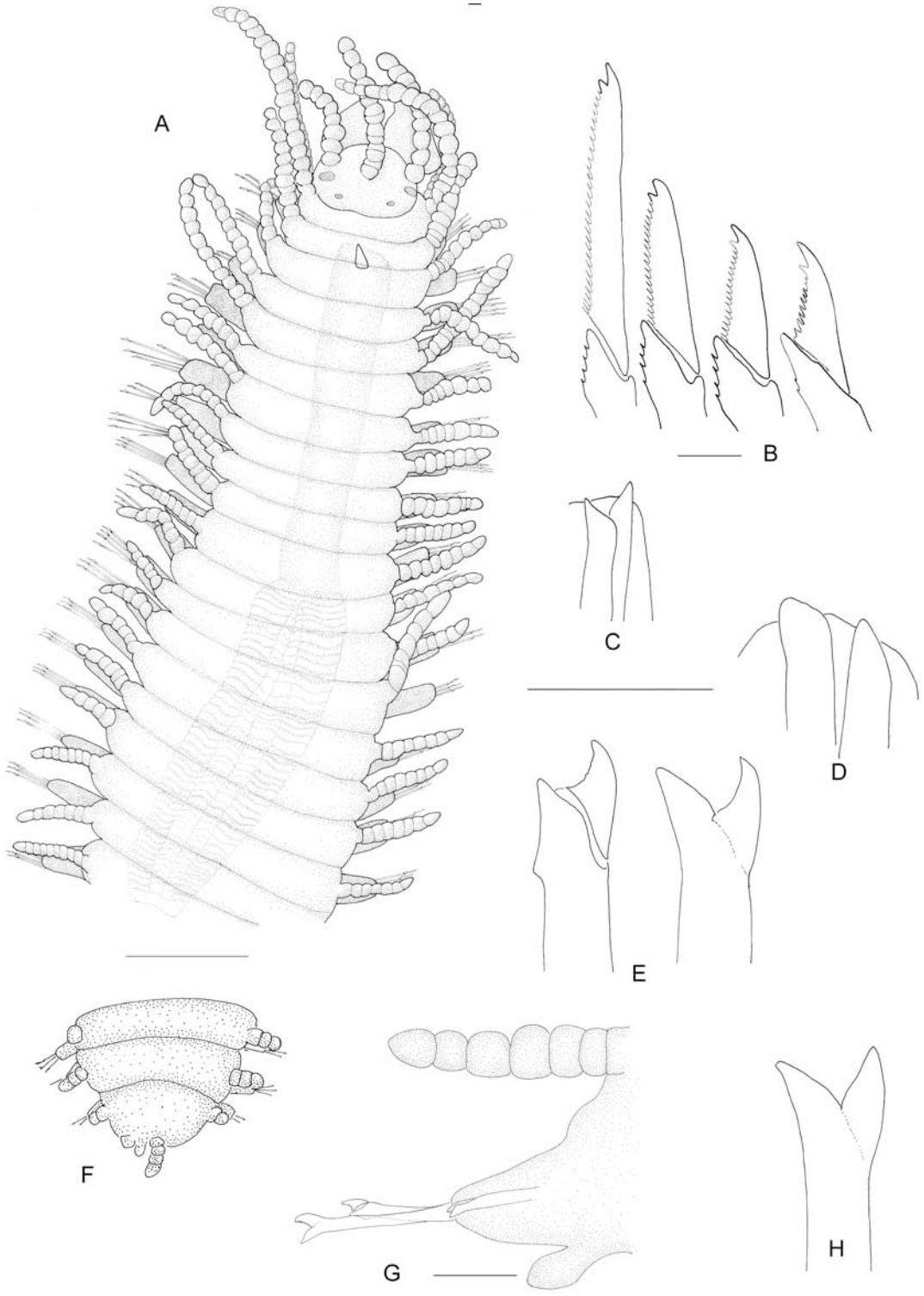

Figure 16. *Syllis ypsiloides* n. sp. Holotype ZMA V. Pol. 5265. A: Anterior part, dorsal view; B: Anterior chaetae; C: Anterior aciculae; D: Posterior aciculae; E: Posterior chaetae; F: Posterior part, dorsal view; G: Posterior parapodium, anterior view; H: Most posterior chaeta. Scale A, F: 0.2 mm; B: 5 μm; C -E, H: 20 μm; G: 48 μm.

antennae, with 18 articles, ventral ones with 13 articles. Anterior-most dorsal cirri with 10-13 articles (Fig. 16A). Midbody and posterior dorsal cirri segments spindle shaped, shorter than anterior ones, with six to eight articles (Fig. 18B). Ventral cirri short, globular, inserted proximally on parapodia, not extending beyond parapodial lobes (Fig. 16G). Anterior parapodia each with six compound, heterogomph chaetae, distal part of shafts provided with spines. Bidentate blades, dorsoventrally decreasing in length (ca. 30 µm dorsal-most, ca. 18 µm ventral-most), moderate long spines on edge of blade (Figs 16B, 17D-F, 18A). Midbody chaetigers with four to five compound chaetae. Blades bidentate, shorter than those present on anterior chaetigers (ca. 25-12 µm), decreasing towards posterior chaetigers. Spines short, gradually decreasing in number and length posteriorly, proximal tooth also decreasing in size becoming almost unidentate. Midbody to posterior chaetigers with two chaetae, one dorsal, ypsiloid simple chaeta originated from fusion of blade and shaft, fusion line barely distinguishable; and one compound ventral chaeta with short unidentate blade (ca. 14 µm), smooth on edge (Figs 16E, 18B-D). Posterior-most chaetigers with only one ypsiloid simple chaeta, fusion line barely visible (Fig. 16H). Two acuminate aciculae per parapodium (Figs 16C, D, 17D). Pygidium conical (Fig. 16F), two anal cirri with eight articles (in paratype). Pharynx similar in length to proventricle; tooth on anterior margin. Proventricle extending through nine segments, with about 40 cell-rows, median longitudinal line visible (Fig. 16A).

Remarks. There are several species sharing these morphological characters such as spindle shaped, short (less than body width) dorsal cirri and bidentate compound chaetae on anterior chaetigers, which change in shape and length towards the posterior part of the body. *Syllis gracilis* and *S. magellanica* both too have ypsiloid simple chaetae from midbody to posterior parapodia. *Syllis ypsiloides* n. sp., has one ypsiloid simple chaeta and one compound ventral chaeta, whereas two ypsiloids are present in *S. gracilis*. Besides, the ypsiloid simple chaetae of *S. gracilis* do not show a fusion line, which is always present in *S. ypsiloides* n. sp. This line reveals that the simple (not-compound) chaetae evolved from a fusion process between the blade and shaft, in a similar way as was proposed for the simple chaetae present in *Haplosyllis anthogorgicola* Utinomi, 1939 (Martin et al., 2002) and in *H. loboi* Paola, San Martín & Martin (2006) (Paola et al., 2006). *Syllis magellanica* has several compound and

ypsiloid chaetae on each posterior parapodia, the latter also showing a fusion line. Another similar species is *S. gracilis australiensis* Hartmann-Schröder, 1979, described from Western Astralia and New South Wales. It was later synonimized with *S. gracilis* by Licher (1999) but we consider that this species might be a valid taxon that should be re-described. *Syllis gracilis australiensis* is similar to *S. ypsiloides* n. sp. in having only one ypsyloid chaeta in addition to one compound on posterior chaetigers (Hartmann-Schröder, 1979). However, it is different principally because the ypsiloid chaetae has spines on the verge while they are completely smooth in *S. ypsiloides* n. sp., and the anterior compound chaetae have a longer and thiner proximal tooth.

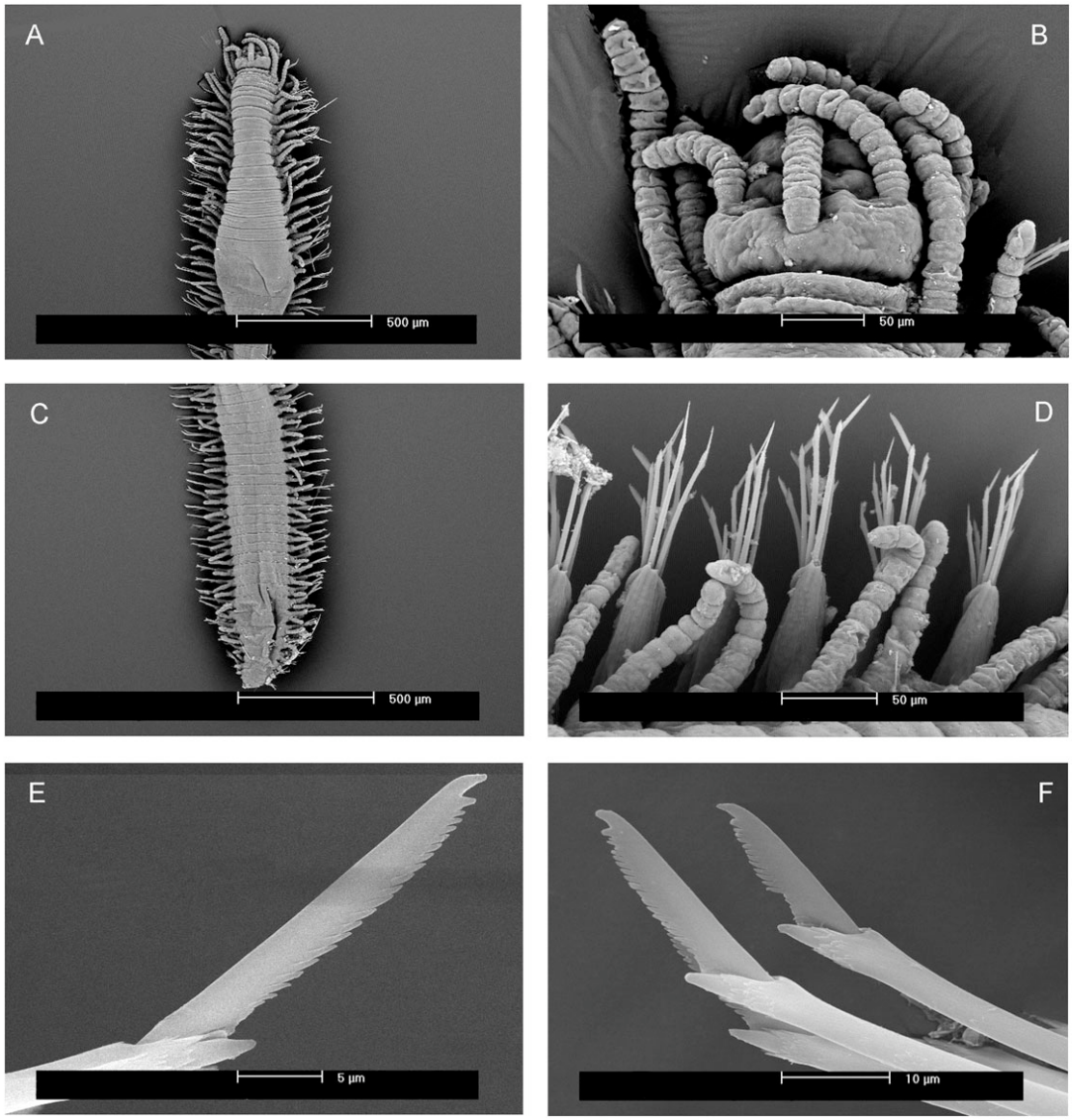

Figure 17. *Syllis ypsiloides* n. sp. Paratype ZMA V. Pol. 5266. SEM. A: Anterior part, dorsal view; B: Prostomium, dorsal view; C: Posterior part, dorsal view; D: Anterior parapodia, dorsal view; E; F: Anterior chaetae.

The simple chaetae of *S. ypsiloides* n. sp. may be related to the habitat in which the species occurs (sponges and corals), as several authors have suggested that acquisition of simple chaetae may be an adaptation to such a symbiotic way of life, as these stout blades could be useful for attachment to the host (Martin & Britayev, 1998). However, such an eco-morphological relationship between shape and function seems difficult to establish without additional research (Musco & Giangrande, 2005).

Distribution. Indonesia.

Etymology. The specific name refers to the ypsiloid chaetae present in the posterior parapodia.

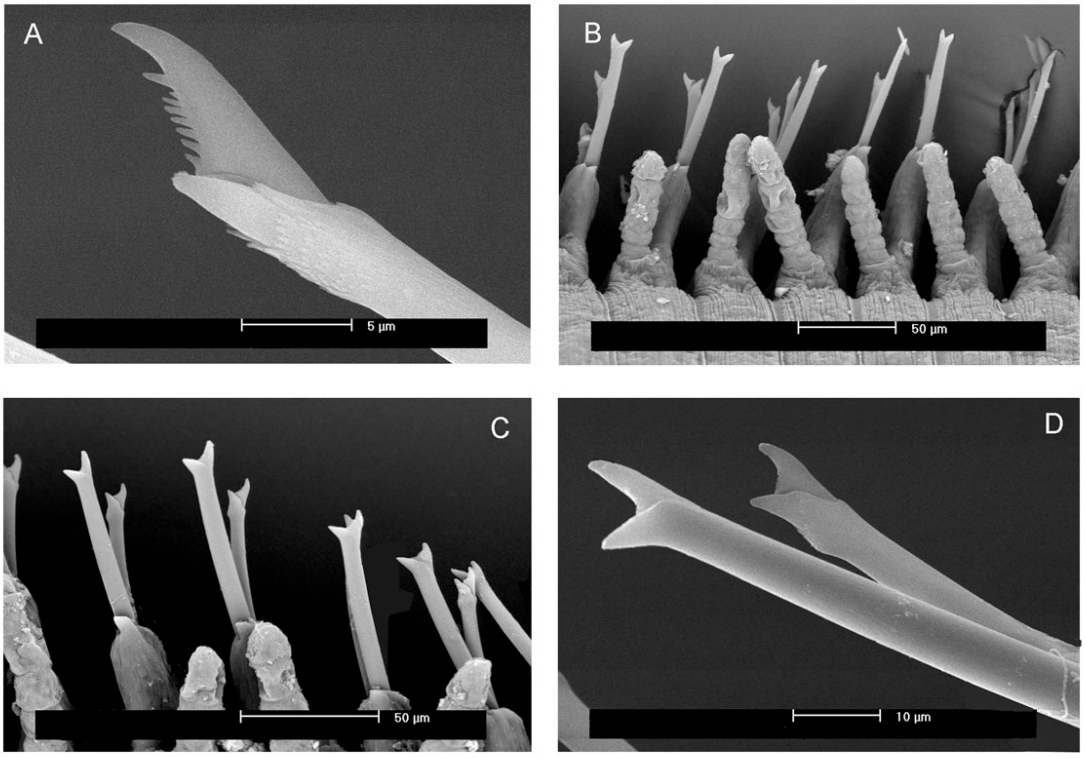

Figure 18. *Syllis ypsiloides* n. sp. Paratype ZMA V. Pol. 5266. SEM. A: Anterior chaeta; B: Posterior parapodia, dorsal view. C, D: Posterior chaetae.

***Syllis* sp. 1**

Fig. 19

Material examined. 1 spec. ZMA V.Pol. 1993 (as *Syllis zonata*), Indonesia, Maluku, Kur Isl., anchorage off Kilsuin, coral, dredge, 20-45m, Siboga Expedition, Sta. 250, 6/7 Dec. 1899.

Description. Specimen incomplete, 12.5 mm long, 0.4 mm wide, with 91 segments. Body circular in cross-section, ventrally flattened. Strongly pigmented dark red. Prostomium wider than long, no visible eyes. Median antenna inserted on middle of prostomium, longer than combined length of prostomium and palps, with 26 articles. Lateral antennae inserted anteriorly, longer than median antenna, with 32 articles. Palps broad, fused at base with distinct median groove, slightly longer than prostomium. Peristomium partially covering prostomium (Fig. 19A). Dorsal tentacular cirri slightly longer than lateral antennae, with 32-45 articles, ventral ones shorter, with 28 articles. Dorsal cirri alternating in length, longer ones with about 45 articles and shorter ones with 22. Articles of anterior dorsal cirri shorter than those of posterior-most dorsal cirri. Cirrophores present on all parapodia. Ventral cirri inserted proximally, conical, not extending beyond parapodia. Parapodia triangular, with pre- and postchaetal lobes similar in length (Fig. 19F). Anterior chaetigers with five to eight compound heterogomph chaetae. Blades bidentate (ca. 25-30 μm) with spines on margin (Fig. 19B). Midbody parapodia with five to six compound chaetae. Blades shorter than those of anterior chaetigers (ca. 20-25 μm), bidentate, both teeth similar in size and length, spines on margin. Shafts with distal spines (Fig. 19C). Posterior parapodia with six compound chaetae, equal in length to blades from midbody chaetigers. Blades bidentate with both teeth similar in size and length, with long marginal spines. Shafts with distal spines (Fig. 19E). One simple dorsal chaeta in posterior chaetigers, straight, with subdistal, short projection (Fig. 19D). Ventral simple chaetae not seen. Four aciculae in anterior parapodia, three straight and blunt and one curved (Fig. 19G). Posterior parapodia with two pointed aciculae (Fig. 19H), one of them protruding beyond parapodia. Pygidium missing. Pharynx long, similar in length to proventricle, extending through 12 segments, with anterior conical tooth. Proventricle long, extending through 11 segments, with about 39 cell-rows (Fig. 19A).

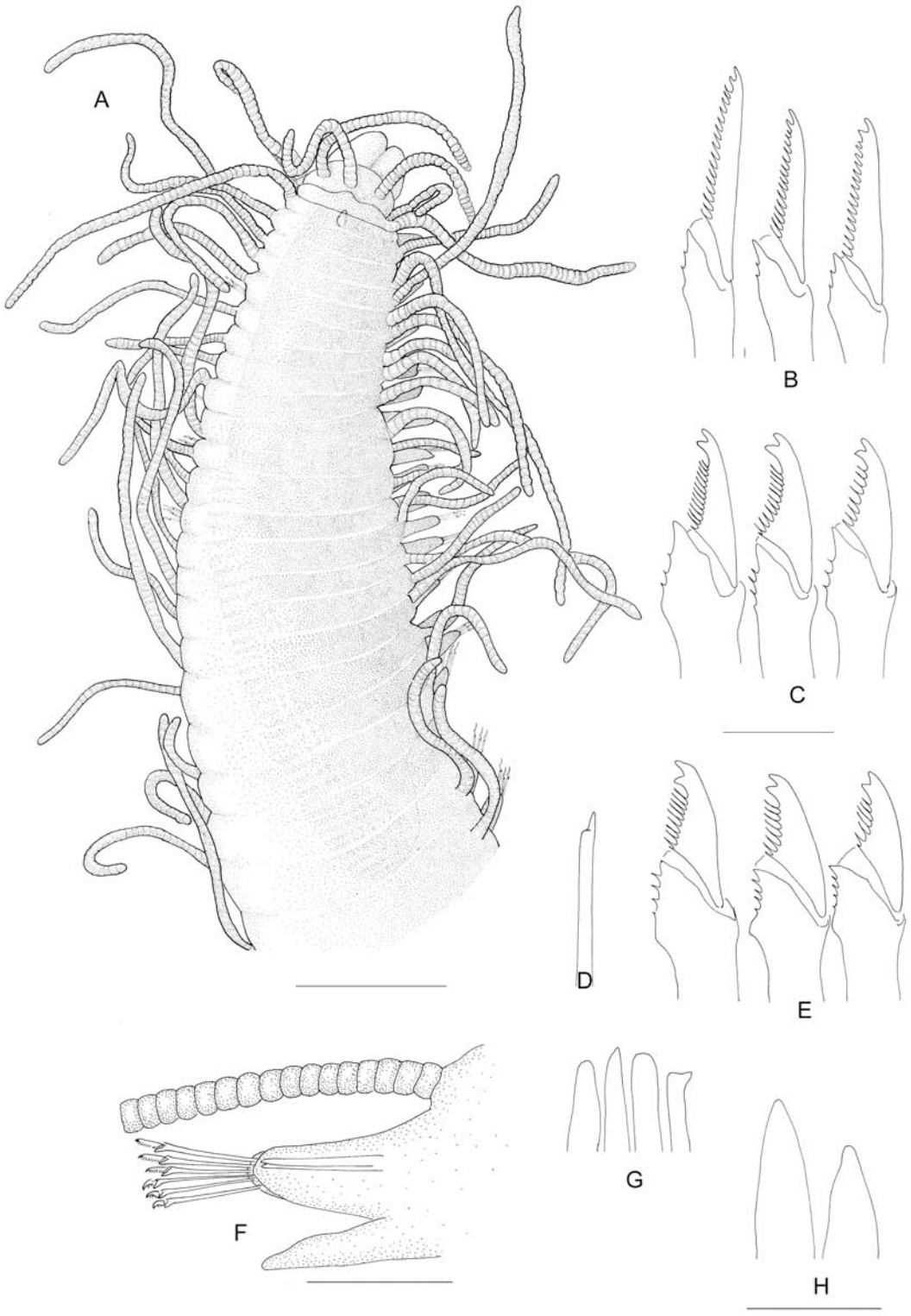

Figure 19. *Syllis* sp. 1. ZMA V. Pol. 1993. A: Anterior part, dorsal view; B: Anterior chaetae; C: Midbody chaetae; D: Dorsal simple chaeta; E: Posterior chaetae; F: Midbody parapodium, anterior view; G: Anterior aciculae; H: Posterior aciculae. Scale A: 0.2 mm; B-E, G-H: 20 μm; F: 1 mm.

Remarks. There are other taxa with long cirri alternating in length and similar chaetae. This specimen is most similar to *Syllis lutea*, but the blades of its midbody and posterior compound chaetae show a proximal tooth considerably wider than the distal one, the spines of the blades are longer and curved, and as long as the proximal tooth (Hartmann-Schröder, 1960, Licher, 1999). In *Syllis* sp. 1, blades of compound chaetae do not have a proximal tooth wider than the distal one and the distal spines, although long, are never as long as the secondary tooth. Similar differences exist between *Syllis* sp. 1 and *S. glarearia*. Blades of compound chaetae in *S. glarearia* also have a wide and long proximal tooth and long spines, of which at least one or two are as long as the proximal tooth. Moreover, *S. glarearia* has bidentate simple dorsal chaetae, unidentate as present in *S.* sp. 1 (Westheide, 1974, Licher, 1999). In *Syllis jorgei* San Martín & López, 2000 (Mediterranean Sea) the long spines of the blades are longer than the distal teeth (San Martín & López, 2000; San Martín, 2003).

The absence of eyes in this species may be a result of the time spent in alcohol. Identification to species is not possible given its condition.

Distribution. Indonesia.

***Syllis* sp. 2**

Fig. 20

Material examined. 1 spec. ZMA V.Pol. 1986.01 (as *S. brachychaeta*), Indonesia, 5º56.7´N 126º25´E, 0-36 m, Siboga Expedition, Sta. 133, 25/27 July 1899.

Comparative material examined.

Syllis gracilis. 1 syntype MPW395, Mediterranean Sea, Adriatic Sea; several spec. MNCN 16.01/ 8927, 8928, 8936, 8938, 8948, Spain, Málaga, Nerja, 36º44’28.85’’N 3º52’47.15’’W, Dec. 1982-Aug. 1983. (identified by San Martín, 2003).

Syllis armillaris. Several spec. MNCN 16.01/7906-07, Spain, Almería, Cabo de Gata, 2 m, 36º46’49.11’’N 2º14’25.31’’W, Jan. 1987. (Identified by San Martín, 2003).

Description. Complete specimen 6.5 mm long, 0.5 mm wide, with 96 segments. Strongly pigmented red. Prostomium wider than long, with two pairs of eyes in trapezoidal arrangement, anterior ones slightly larger than posterior. Median antenna inserted on middle of prostomium, similar in length to combined length of prostomium

and palps, with 19 articles; lateral antennae shorter, inserted on anterior margin of prostomium, with 11 articles. Palps triangular, longer than prostomium, fused at base, with distinct median groove (Fig. 20A). Peristomium shorter than subsequent segments, with two pairs of tentacular cirri. Dorsal tentacular cirri longer than lateral antennae, with 17 articles, ventral ones with 10-11 articles. Dorsal cirri of most anterior segments with 25-26 articles. Midbody and posterior dorsal cirri shorter than anterior ones, varying slightly in length, alternately with 10 and 8 articles (Fig. 20A). Ventral cirri digitiform, inserted proximally to parapodia, not extending beyond parapodial lobes (Fig. 20K). Anterior parapodia with ten compound, heterogomph chaetae, distal part of shafts provided with spines. Blades bidentate, decreasing in length (ca. 23 μm dorsal-most, ca. 18 μm ventral-most), long spines on edge (Fig. 20B). Midbody parapodia with five compound chaetae, blades bidentate, shorter than those of anterior chaetigers (ca. 15-13 μm), gradually decreasing in length posteriorly (ca. 11-9 μm), and shafts becoming thicker (Fig. 20D). Spines on margin short, decreasing posteriorly in number, proximal tooth also decreasing in size to become almost unidentate (Fig. 20D). Posterior chaetigers with three to four compound unidentate chaetae, blades short with distal end curved and proximal edge large, more developed than those of anterior chaetigers, short and thin spines on edge (Fig. 20F). Shafts large and strong, distal end curved. Blades and shafts on posterior chaetae in close contact but not fused (Fig. 20F); dorsal-most blade smallest, and more clearly separated from shaft than ventral-most (Fig. 20F). Posterior chaetigers with one dorsal simple chaeta, straight and weakly bidentate (Fig. 20G), and one ventral simple bidentate chaeta, slightly curved distally (Fig. 15H). Two acuminate aciculae per parapodium (Figs 20C, E, I). Pygidium conical, two anal cirri with 18 articles (Fig. 20J). Pharynx extending through eight segments; conical tooth on anterior margin. Proventricle extending through nine segments, cell-rows difficult to distinguish (Fig. 20A).

Remarks. Syllis sp. 2 is principally characterized by the shape of the posterior compound chaetae, considerably shorter than the anterior ones, tending to an ypsiloid condition, although blades are never fused with the shafts. *Syllis* sp. 2 is similar to *Syllis gracilis* and other species having ypsiloid chaetae in midbody to posterior parapodia, originating from enlarged shafts fused with blades, and having short, spindle-shaped dorsal cirri. *Syllis gracilis* has only two large ypsiloid chaetae (with fused blades) on midbody to posterior parapodia. In addition, the posterior compound chaetae of *Syllis*

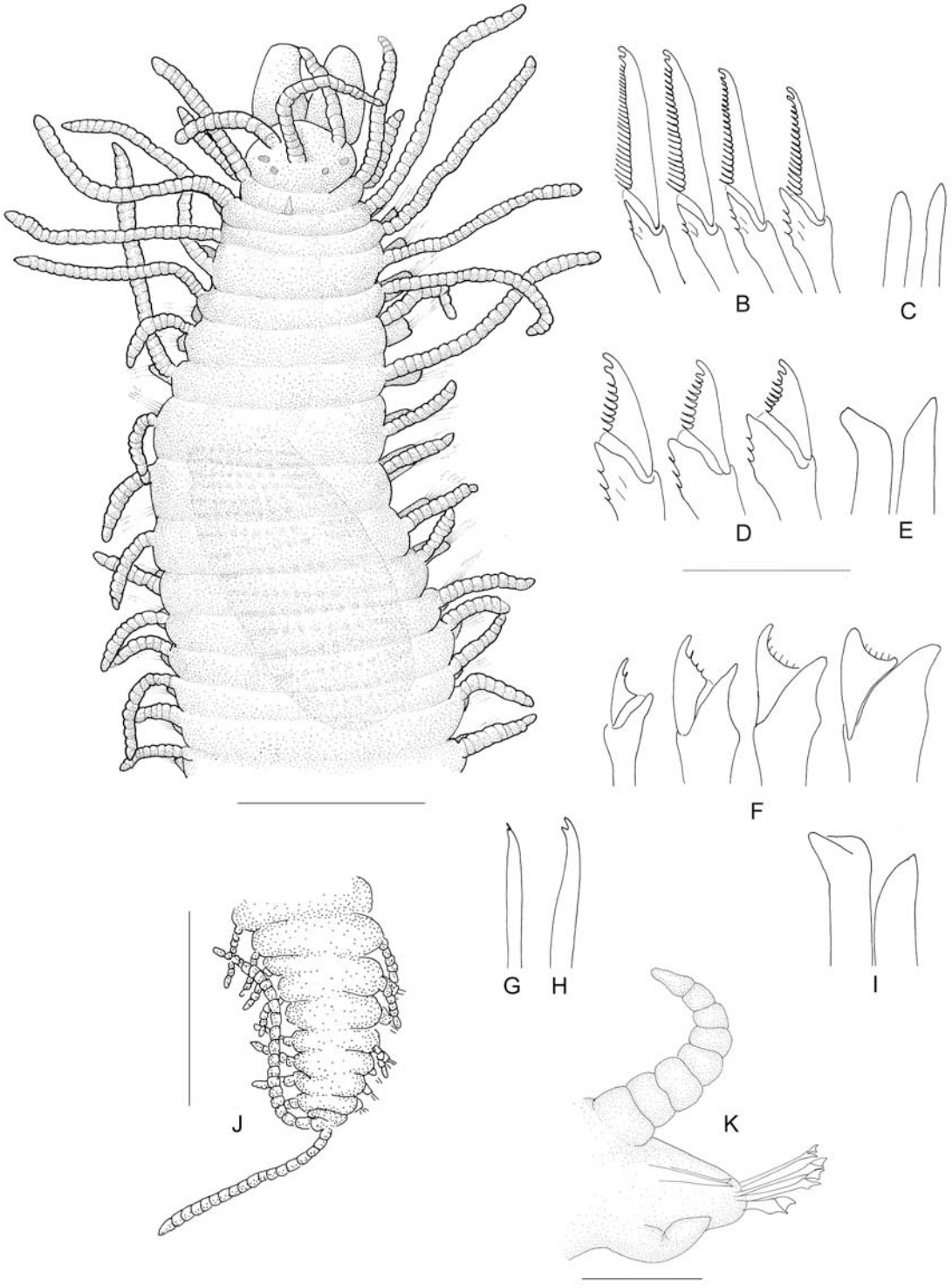

Figure 20. *Syllis* sp. 2. ZMA V. Pol. 1986.01. A: Anterior part, dorsal view; B: Anterior chaetae; C: Anterior aciculae; D: Midbody chaetae; E: Midbody aciculae; F: Posterior chaetae; G: Dorsal simple chaeta; H: Ventral simple chaeta; I: Posterior aciculae; J: Posterior part, dorsal view; K: Midbody parapodium, anterior view. Scale A, J: 0.4 mm; B-I: 20 µm; K: 48 µm.

sp. 2 have an unusual inverse gradation in length, the dorsal blades being more slender and shorter than the ventral ones (Figs 20F, K). *Syllis armillaris* presents in midbody to posterior parapodia compound chaetae with short, unidentate blades never fused. *Syllis mayeri* is another similar species, but its anterior dorsal cirri are longer, the spines of the blades in anterior chaetae are shorter and one of the two midbody aciculae is larger (Musco & Giangrande, 2005). Also the compound chaetae exhibit the common condition of gradation in size and length with longer blades dorsally, shorter ones ventrally. Other similar species are *S. magellanica*, which presents ypsiloid chaetae together with compound chaetae, and *S. ypsiloides* n. sp. (see remarks of that species in this study).

The specimen is a complete adult, and is different from other species of the genus. Syllid species with simple chaetae formed from a fusion process between shaft and blade occur in different body regions. We cannot exclude the possibility that a specimen may undergo such a fusion process only later in life. Thus not knowing the possible range of variation in this case, we are of the opinion that this single specimen better should not be formally named as a new species unless additional material is found.

Distribution. Indonesia.

***Syllis* sp.**

Material examined. 1 spec. ZMA V.Pol. 5279 (ex ZMA V.Pol. 1985.03 as *Syllis exilis*), Indonesia, 8º30´S 119º7.5´E, 73 m, Siboga Expedition, Sta. 310, 12 Feb. 1900; 1 spec. ZMA V.Pol. 2019.01 (as *Syllis variegata*), Indonesia, Sulu Archipelago, SE side of Peral Bank, 125 m, Siboga Expedition, Sta. 96, 27 June 1899; 1 spec. ZMA V.Pol. 2019.02 (as *Syllis variegata*), Indonesia, 6º7.5´N 120º26´E. 16-23 m, Siboga Expedition, Sta. 99, 28/30 June 1899; 1 spec. ZMA V.Pol. 1986.04 (as *Syllis brachychaeta*), Indonesia, 9º10.3´S 125º55.1´E, 421 m, Siboga Expedition, Sta. 291, 20 Jan. 1900; 1 spec. ZMA V.Pol. 2234 (identified by Augener as *Syllis cerina*), Indonesia, 0º7.2´N 130º25.5´E, 82 m, Siboga Expedition, Sta. 154, 14 Aug. 1899; 1 spec. ZMA V.Pol. 2211.01 (as *Syllis sexoculata*), Indonesia, 3º27´S 117º36´E, 59 m, Siboga Expedition, Sta. 77, 10 June 1899; 1 spec. ZMA V.Pol. 5268, Indonesia, NE coast of Sumba, 09°57'S 120°49'E, 45 m, sandy bottom and sponges, Snellius II, Sta. 4.067, 16 Sept. 1984. 1 spec. ZMA V.Pol. 5269, Indonesia, NE coast of Sumba, E. of Melolo,

09°53.5'S 120°42.7'E, calcareous stones, rich epifauna dominated by soft corals, 75-90 m, Snellius II, Sta. 4.051, 13 Sept. 1984.

Remarks. Specimens in poor condition, in many cases only fragments or juveniles. A more complete identification is not possible.

Genus *Trypanosyllis* Claparède, 1864

Trypanosyllis Claparède, 1864: 558.- San Martín, 2003: 307.

Parautolytus Ehlers, 1900: 213.

Type species. *Syllis zebra* Grube, 1860.

***Trypanosyllis zebra* (Grube, 1860)**

Syllis zebra Grube, 1860: 86, pl. 3, fig. 7.

Trypanosyllis zebra. - Langerhans 1879: 556. - Haswell 1920: 101. - Fauvel 1923: 269, figs 101 a-e. - Day 1967: 256, figs 12.6. a-b. - San Martín 2003: 311, figs 171-173.

Trypanosyllis krohnii Claparède, 1864: 558, pl. 7, fig. 2.

Syllis taeniaformis Haswell, 1886: 741, pl. 1, figs 4, 5.

Trypanosyllis taeniaformis. - Augener 1913: 230. - Westheide 1974: 39, figs 16a-d.

Trypanosyllis (Trypanedenta) taeniaformis. - Imajima & Hartman 1964: 127, figs 30 h-k. - Imajima 1966: 239, figs 45 a-i. - Hartmann-Schröder 1989: 18.

Trypanosyllis richardi Gravier, 1900: 168, pl. 9, figs 12, 13.

Trypanosyllis vittigera Ehlers, 1887: 151, pl. 40, figs 1-3. - Uebelacker 1984: 30.88, figs 30.81, 82a-h.

Parautolytus luzenensis Pillai, 1965: 123, figs 5e-i, 6a-c.

Material examined. 1 spec. ZMA V.Pol. 5270, Indonesia, Komodo, NE Cape, 08°29'S 119°34.1'E, sandy bottom, algae, occasional sponges and tunicates, 30-34 m, Snellius II, Sta. 4.096d, 19-20 Sept. 1984.

Remarks. The specimen agrees well with the previous descriptions. After San Martín (2003), *Trypanosyllis richardi* Gravier, 1900 (Red Sea), *T. taeniaformis* Haswell, 1886 (Western Australia) and *T. vittigera* Ehlers, 1887 (Caribbean Sea) are considered to be synomyms of *T. zebra*. Nevertheless, a revision of the material of *T. zebra*, as well as the other nominal species, is required in order to clarify the wide geographical

distribution of this taxon.

Distribution. East Atlantic Ocean (English Channel to South Africa), Mediterranean Sea, Caribbean, Red Sea, Indonesia and Pacific Ocean.

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Syllidae (Polychaeta) from Lebanon with two new reports for the Mediterranean Sea

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Abstract: A collection of 24 samples from Lebanon (Eastern Mediterranean Sea) was studied yielding a number of 27 identified species. Two of them: *Exogone breviantennata* Hartmann-Schröder, 1959 and *Syllis bella* (Chamberlin, 1919) are new reports for the Mediterranean Sea. One more species, *Inermosyllis balearica* (San Martín, 1982) is a new report for the Eastern area. Another species *Syllis* cf. *mayeri* has been found but its identification is not completely certain. Similarities and differences with *Syllis mayeri* Musco & Giangrande, 2005 are exposed. A discussion about possible migration explanations to the presence in the Mediterranean of these species is included.

Résumé : *Syllidae (Polychaeta) des côtes du Liban, dont deux espèces nouvelles pour la Méditerranée.* Une collection de 24 échantillons provenant du Liban (Mer Méditerranéenne orientale) a été étudiée, permettant l'identification de 27 espèces de Syllidés. Deux d'entre elles : *Exogone breviantennata* Hartmann-Schröder, 1959 et *Syllis bella* (Chamberlin, 1919) sont nouvelles pour la Mer Méditerranée. Une espèce, *Inermosyllis balearica* (San Martín, 1982), est nouvelle pour le secteur oriental. Une autre espèce, *Syllis* cf. *mayeri*, a été trouvée mais son identification n'est pas encore validée. Des similitudes et des différences avec les *Syllis mayeri* Musco et Giangrande, 2005 sont exposées. Les causes possibles de cette migration expliquant la présence de ces espèces en Méditerranée sont discutées.

Keywords: Syllidae • Polychaeta • Taxonomy • New reports • Mediterranean Sea

Introduction

The Syllidae (Polychaeta) from Eastern Mediterranean Sea have been studied by several authors, especially during the last years. There are several ecological studies, faunistic analyses, and newly described species of Syllidae from the Aegean Sea (Çinar & Ergen, 2002; Çinar, 2003a; Çinar, 2005). Syllids and other polychaetes from the Suez Canal were studied by Ben-Eliahu (1972a). Polychaete faunas from Israel and the Gulf of Elat have been extensively studied in several works (Tebble, 1959; Day, 1965; Ben-Eliahu, 1975, 1976a, 1976b & 1976c; Ben-Eliahu & Fiege, 1995). Syllids from the same area were specifically studied by Ben-Eliahu (1977a & 1977b) and Harlock & Laubier

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(1966). Polychaetes from Beirut, the Lebanon, were studied by Laubier (1966), and those from Turkey by Ergen (1976) and Çinar (1999). Fauvel (1933 & 1937) studied the polychaetes from Egypt. A checklist, distribution, and ecological features of Syllidae and other polychaetes from Greece can be consulted in Simboura & Nicolaidou (2001). New species, ecology and systematic studies on polychaetes, including Syllidae, from Cyprus are those of Ben-Eliahu (1972b), Çinar (2003b), Çinar & Ergen (2003), Çinar et al. (2003), and more recently Musco et al. (2005). Finally, a broad biogeographic revision on Syllidae from the Mediterranean Sea (East and West areas) was carried out by Musco & Giangrande (2005a).

Numerous studies have recently stressed the introduction of foreign organisms into marine communities. Nishi & Kato (2004) studied the nature of introduced or cryptogenic species of polychaetes around the world, and concluded that Spionidae, Sabellidae, Serpulidae and Nereididae are the most frequent. In some instances, both the origin and the area of introduction were considerably distant (e.g. from South Africa, or Australia to Italy; from South Africa to the Pacific side of U.S.A.; from Western Europe to Japan). Several species have also been reported as introduced at the Northern Baltic Sea (Stigzelius et al., 1997). There are several reports about the Lessepsian migrations specific to the Eastern Mediterranean (i.e. from Red Sea to the Mediterranean through the Suez Canal) (Ben-Eliahu, 1972c; Por, 1971, 1978 & 1990; Ergen et al., 2002; Ergev et al., 2003; Çinar & Ergen, 2005; Çinar et al., 2006). Studies about alien species of invertebrates and vertebrates marine groups in the Mediterranean Sea are those of Çinar et al. (2005), Zenetos et al. (2005), and Çinar (2006). All coincide in considering the introduction of species as a relatively common process, despite information might sometimes be limited. While some introduction vectors have been hypothesized, (e.g. ballast water and fouled ships; Nishi & Kato, 2004), we do not really have concise data detailing how this happens, or how long and stable these introduction processes are. Furthermore, the geographic distribution of many species of polychaetes is often discontinuous, likely because there are still numerous poorly known areas around the world. This, hence, makes the tracking of species displacements along the globe more difficult.

We have studied a collection of Syllidae from Lebanon. The material was collected by Ghazi Bitar, Helmut Zibrowius and Michel Bariche, and is currently cured by Dr. Dieter Fiege at the Senckenberg Museum. Most of the revised species are well known, common and widely reported for the Mediterranean, as well as for the Levant Basin. However, there are two species previously unreported for the Mediterranean, plus one additional species previously reported only for the Western Mediterranean (but new for the Eastern basin). In this paper we offer a taxonomic account for the species found in order to contribute to a better knowledge of the Syllidae from Easter Mediterranean. We also include detailed descriptions, drawings, and SEM photographs of the most interesting species. The Eastern Basin is a geographical area in which many examples of new invasions have been already reported. In special, several events of accidental introductions by ships and Lessepsian migrations have been reported in the last years. We thereby include a discussion about the possible origin of our new reports for the Mediterranean.

Material and Methods

All the samples were collected during field trips in October 1999, May and June 2000, April 2001, September 2002, and July 2003. The samples were fixed in 10% formaldehyde-seawater solution and preserved in 70% alcohol solution. For identification, an Olympus SZ30 stereomicroscope and Olympus CH30 optic microscope were used. Drawings were made using a drawing tube in a Nikon Optiphot optic microscope equipped with interference contrast system (Nomarski). Selected specimens were critical point dried and subsequently coated with 102 Å of gold for SEM. Examination was taken with Philips XL30 electronic microscope, connected to an EDAX DX4i analyzer at SIDI (Servicio Interdepartamental de Investigación), Universidad Autónoma de Madrid (UAM). Width of the specimens was measured at level of proventricle, excluding parapodia. All the studied material is deposited at the Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt (SMF). Comparative material examined has been loaned by the Museo Nacional de Ciencias Naturales de Madrid, Spain (MNCN), the Australian Museum (AM) and the Muzeum Przyrodnicze Wroclaw, Poland (MPW).

Results

AUTOLYTINAE Langerhans, 1879

Myrianida prolifera (Müller, 1788)

Autolytus prolifer San Martín, 2003: 489-492, figs 269, 270.
Myrianida prolifera Nygren, 2004: 151-152, fig. 75A-E.

Material examined

1 specimen (SMF16470), Selaata, small caves and overhangs, 3-8 m, 18.x.1999. 1 specimen (SMF16468), Ras el Chakaa, cliff, 4-8 m, 19.x.1999.

Distribution

North East Atlantic Ocean. Mediterranean Sea.

Proceraea aurantiaca Claparède, 1864

Proceraea aurantiaca San Martín, 2003: 473-475, figs 259, 260 (in part). Çinar *et al.*, 2003: 748. Nygren, 2004: 44-45, fig. 6A-E.

Material examined

1 specimen (SMF16403), Selaata, small caves and overhangs, 3-8 m, 18.x.1999.

Distribution

North East Atlantic Ocean. Mediterranean Sea.

EUSYLLINAE Malaquin, 1893

Eusyllis kupfferi Langerhans, 1879

Eusyllis kupfferi Langerhans, 1879: 552, fig. 14. San Martín, 1990: 607, figs 12, 13. Çinar & Ergen, 2003: 177-178, fig. 1. San Martín & Hutchings, 2006: 276-278, figs 12D-F, 13A-G, 14A-E.

Material examined

1 specimen (SMF16399), Selaata, small caves and overhangs, 3-8 m, 18.x.1999. 1 specimen (SMF16428), Beirut, Harf el Kalb, overhangs, 34 m, 21.x.1999. 1 specimen (SMF16445), El Kassmieh, cliff with *Madracis pharensis*, 42-43 m, 25.x.1999. 1 specimen (SMF16351) and 1 specimen (SMF16362), Batroun, encrusted cliff, 9 m, 16.x.1999. 1 specimen (SMF16439), Ramkine Island, cave, 5-7 m, 31.v.2000.

Comparative material examined

4 specimens (AM W28218), Australia, New South Wales, Off old wharf, Richmond R., near Ballina, 28°52.5'S 153°33.6'E, drift algae, 6 m, 5.iii.1992.

Remarks

Eusyllis kupfferi is characterized by having net-shaped dorsal simple chaetae and compound chaetae with blades short, distally curved and unidentate. The examined specimens agree well with a recent description and iconography of same species made by the second author (San Martín & Hutchings, 2006). This species was described from Madeira (Langerhans, 1879) and reported on the Canary Islands (Núñez & San Martín, 1996), Cuba (San Martín, 1990) and Australia (San Martín & Hutchings, 2006) and was recently found in the Eastern Mediterranean Sea (Çinar & Ergen, 2003).

Distribution

Atlantic Ocean (Madeira, Canary Islands, Cuba). Australia (Queensland, Western Australia, New South Wales). Mediterranean Sea.

Eusyllis lamelligera Marion & Bobretzky, 1875

Eusyllis lamelligera Marion & Bobretzky, 1875: 33, pl. 3, figs 9A-C. San Martín, 2003: 117, figs 54, 55. Çinar & Ergen, 2003: 772-773. San Martín & Hutchings, 2006: 278-280, figs 15A-J, 16A-F.

Material examined

1 specimen (SMF16348), Ramkine Island, with crust and corals, 13 m, 22.x.1999. 3 specimens (SMF16367), Batroun, encrusted cliff, 9 m, 16.x.1999.

Distribution

North Atlantic. Australia (Atlantic and Pacific coasts). Mediterranean Sea.

Odontosyllis fulgurans
(Audouin & Milne Edwards, 1833)

Odontosyllis fulgurans Audouin & Milne Edwards, 1833: 229. San Martín, 2003: 104-106, fig. 46. Çinar & Ergen, 2003: 773.

Material examined

1 specimen (SMF16407), Ramkine Island, cave, 5-7 m, 31.v.2000. 3 specimens (SMF16456), Khaldeh, marina Villamar, with *Caulerpa scalpelliformis*, 1-2 m, 7.vi.2000. 2 specimens (SMF16373), Kfar Abida, 7-8 m, 30.v.2000. 1 specimen (SMF16353), Batroun, encrusted cliff, 9 m, 16.x.1999.

Distribution

Apparently cosmopolitan.

EXOGONINAE Langerhans, 1879

Exogone breviantennata Hartmann-Schröder, 1959

Exogone breviantennata Hartmann-Schröder, 1959: 125, figs 75-78.
Exogone (Exogone) breviantennata San Martín, 1991: 730, fig. 8; 2005: 141-142, figs 81A, 89A-I.

Material examined

2 specimens (SMF16384), Ras El Chakaa, cliff, 4-8 m, 19.x.1999. 1 specimen (SMF16390), Beirut harbour, 3-8 m,

2.vi.2000. 6 specimens (SMF16354), Batroun, encrusted cliff, 9 m, 16.x.1999.

Comparative material examined

4 specimens (AM W26457), Australia, Queensland: lagoon entrance, Lizard Island, 14º40'S 145º28'E, medium to fine sediment, 18m, 9.x.1978.

Description

Body long, slender. Prostomium wider than long; 4 eyes in trapezoidal arrangement. Antennae papilliform, inserted between anterior eyes, median antenna slightly longer than lateral ones. Palps longer than prostomium, completely fused, with a dorsal furrow and a distal notch. Tentacular cirri papilliform. Dorsal cirri small, similar to lateral antennae, present on all segments. Parapodia with one compound chaeta, blade spiniger-like, bidentate, with long marginal spines, shaft with subdistal spines and 4 compound falcigers, blades bidentate, proximal tooth larger than distal one, and long marginal spines, shafts with subdistal spines. Dorsal simple chaetae slender, bidentate, with small marginal spines. Ventral simple chaetae sigmoid, bidentate, smooth. One acicula per parapodium, distally rounded. Pharynx through 4 segments; pharyngeal tooth on anterior end. Proventricle short, through 2 segments.

Remarks

This species is similar to *Exogone verugera* but in *E. breviantennata* the proventricle is distinctly shorter and it has dorsal cirri on the second chaetiger (San Martín, 2003; 2005). The examined specimens agree well with a recent detailed description and iconography of the same species made by the second author (San Martín, 2005). Therefore, we do not consider necessary to include herein a more detailed study of the specimens. This is a new report for the Mediterranean Sea.

Distribution

Apparently circumtropical.

Sphaerosyllis pirifera Claparède, 1868

Sphaerosyllis pirifera Claparède, 1868: 205. San Martín, 2003: 212-216, figs 111-113. Çinar et al., 2003: 759.

Material examined

25 specimens (SMF16363), Batroun, encrusted cliff, 9 m, 16.x.1999. 1 specimen (SMF16440) and 1 specimen (SMF16415), Ramkine island, cave, 5-7 m, 31.v.2000. 1 specimen (SMF16455), Khaldeh, marina Villamar, with *Caulerpa scalpelliformis*, 1-2 m, 7.vi.2000. 2 specimens (SMF16375), Kfar Abida, 7-8 m, 30.v.2000. 1 specimen (SMF16422), Selaata, small caves and overhangs, 6-7 m, 23.x.1999. 1 specimen (SMF16417), El Heri, marina Beaulieu, 2-3 m, 3.vi.2000. 1 specimen (SMF16400), Selaata, small caves and overhangs, 3-8 m, 18.x.1999.

Distribution

Mediterranean Sea. East Atlantic Ocean (Iberian coasts).

SYLLINAE Grube, 1850

Branchiosyllis exilis (Gravier, 1900)

Syllis (Typosyllis) exilis Gravier, 1900: 160, figs 28-30.
Branchiosyllis exilis San Martín, 2003: 332, figs 184, 185. Çinar & Ergen, 2003: 776.

Material examined

3 specimens (SMF16416), El Heri, marina Beaulieu, 2-3 m, 3.vi.2000. 1 specimen (SMF16408), Ramkine Island, cave, 5-7 m, 31.v.2000. 9 specimens (SMF16405) and 1 specimen (SMF16388), Selaata, small caves and overhangs, 3-8 m, 18.x.1999. 1 specimen (SMF16420), Jbail Harbour, 1-2 m, 17.x.1999. 1 specimen (SMF16419), Jbail, Tablieh, 15-16 m, 17.x.1999. 1 specimen (SMF16429), Beirut, marina of Hotel Riviera, with algae, 2m, 21.x.1999. 2 specimens (SMF 16433), Batroun, among epifauna of *Chama pacifica*, 15.x.1999. 1 specimen (SMF16451), Ras el Chakaa, cave, 5-6 m, 4.vi.2000. 3 specimens (SMF16345), Ramkine Island, hardground, 13-14 m, 22.x.1999. 1 specimen (SMF16372), Kfar Abida, 7-8 m, 30.v.2000. 9 specimens (SMF16379), Ras El Chakaa, cliff, 4-8 m, 19.x.1999. 1 specimen (SMF16392), Beirut harbour, 3-8 m, 2.vi.2000. 6 specimens (SMF16358), Batroun, encrusted cliff, 9 m, 16.x.1999.

Distribution

Apparently circumtropical, also present in the Mediterranean Sea.

Eurysyllis tuberculata Ehlers, 1864

Eurysyllis tuberculata Ehlers, 1864: 264, figs 4-7. San Martín, 2003: 296, figs 162-164. Çinar & Ergen, 2003: 776.

Material examined

1 specimen (SMF16357), Batroun, encrusted cliff, 9 m, 16.x.1999.

Distribution

Red Sea. East Atlantic Ocean (Canary Islands), North West Atlantic Ocean (North Carolina to Gulf of México). Mediterranean Sea.

Inermosyllis balearica (San Martín, 1982)

Pseudosyllides balearica San Martín, 1982: 21.
Inermosyllis balearica San Martín, 2003: 326-329, figs 181, 182.

Material examined

1 specimen (SMF16361), Batroun, encrusted cliff, 9 m, 16.x.1999.

Remarks

The specimen agrees well with the descriptions. This species was previously only known for the Western Mediterranean (Iberian coasts, Balearic and Chafarinas Islands), this is the first report in the Eastern basin. Several species of syllids currently present in Western and Eastern basins were previously studied and reported only for the Western area. It could be because the Western area had been more exhaustively studied. Some authors also consider that syllids distribution suggests the existence of an "atlantism" gradient, decreasing eastwards and possibly corresponding to a temperature gradient (Musco & Giangrande, 2005a). However, the number of studies on polychaetes, and syllids in particular, in the Eastern basin has been highly increased during last years and many species that were only known for the Western part are now considered common in both areas. *Inermosyllis balearica* could be another example of species that has probably expanded its distribution from Western waters to Eastern areas of the Mediterranean Sea.

Distribution

Mediterranean Sea.

Opisthosyllis brunnea langerhans, 1879

Opisthosyllis brunnea Langerhans, 1879: 541. San Martín, 2003: 330-331, fig. 183.

Material examined

1 specimen (SMF16421), Enfeh, rock, 8-9 m, rocky shore, 26.x.1999.

Distribution

Atlantic Ocean (Madeira Island to South Africa). Indian Ocean (Mozambique, Somalia, Australia). Pacific Ocean (Japan, Korea & Panam.). Mediterranean Sea.

Syllis armillaris (Müller, 1771)

Nereis armillaris Müller, 1771: 150.
Typosyllis armillaris Licher, 1999: 189-199, fig. 84.
Syllis armillaris San Martín, 2003: 423-426, figs 232, 233. Çinar & Ergen, 2003: 778. Musco & Giangrande, 2005b: 472-473, fig. 4.

Material examined

3 specimens (SMF16418), El Heri, marina Beaulieu, 2-3 m, 3.vi.2000. 10 specimens (SMF16410), Ramkine Island, cave, 5-7 m, 31.v.2000. 3 specimens (SMF16389) and 13 specimens (SMF16406), Selaata, small caves and overhangs, 3-8 m, 18.x.1999. 2 specimens (SMF16423), Selaata, small caves and overhangs, 6-7 m, 23.x.1999. 1 specimen (SMF16435), Beirut harbour, 3-8 m, 2.vi.2000. 1 specimen (SMF16454), Khaldeh, marina Villamar, with *Caulerpa scalpelliformis*, 1-2 m, 7.vi.2000. 3 specimens (SMF16449), Ramkine Island, with barnacles, 3 m, 31.v.2000. 2 specimens (SMF16444), El Kassmieh, cliff with *Madracis pharensis*, 42-43 m, 25.x.1999. 9 specimens (SMF16425), Barbara, overhang, 26 m, 8.vi.2000. 3 specimens (SMF16347), Ramkine Island, hardground, 13-14 m, 22.x.1999. 2 specimens (SMF16380), Ras El Chakaa, cliff 4-8 m, 19.x.1999. 1 specimen (SMF16365), Batroun, encrusted cliff, 9 m, 16.x.1999.

Distribution

Apparently cosmopolitan.

Syllis bella (Chamberlin, 1919)
(Figs 1-3)

Typosyllis bella Chamberlin, 1919: 7. Licher, 1999: 94-96, fig. 45.
Syllis bella Capa et al., 2001: 107.

Material examined

35 specimens (SMF16434), Beirut harbour, 3-8 m, 2.vi.2000. 1 specimen (SMF16457), Khaldeh, marina Villamar, with *Caulerpa scalpelliformis*, 1-2 m, 7.vi.2000. 1 specimen (SMF16450), Ramkine Island, with barnacles, 3 m, 31.v.2000. 1 specimen (SMF16369), Kfar Abida, 7-8 m, 30.v.2000. 2 specimens (SMF16385) and 1 specimen (SMF16398), Ras El Chakaa, cliff, 4-8 m, 19.x.1999. 4 specimens (SMF16364), Batroun, encrusted cliff, 9 m, 16.x.1999.

Comparative material examined

Numerous specimens from Pacific of Panamá (Capa *et al.* 2001).

Description

One of longest specimen 12 mm long, 1 mm wide, with 56 segments. Body long, cylindrical in section, ventrally flattened. Dorsal colour pattern consisting in red pigmentation principally distributed on anterior and posterior parts of each segment forming transversal lines and also a medial

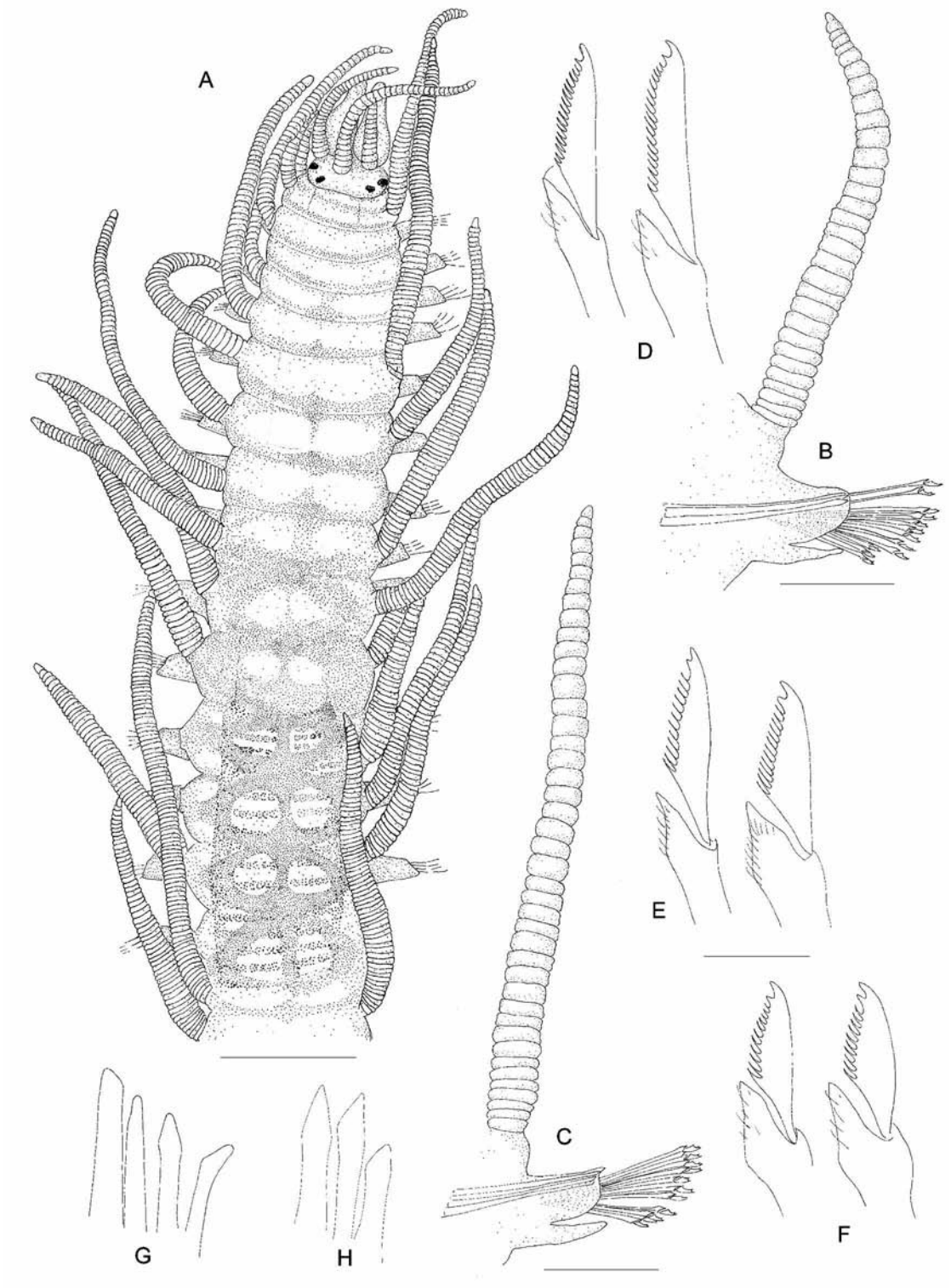

Figure 1. ***Syllis bella*. A.** Anterior part, dorsal view. **B.** Posterior parapodium, anterior view. **C.** Midbody parapodium, anterior view. **D.** Anterior chaetae. **E.** Midbody chaetae. **F.** Posterior chaetae. **G.** Anterior aciculae. **H.** Posterior aciculae. Scale: A, 0.5 mm; B, C, 0.2 mm; D-H, 20 µm.

Figure 1. ***Syllis bella*. A.** Partie antérieure, vue dorsale. **B.** Parapode postérieur, vue antérieure. **C.** Parapode moyen, vue antérieure. **D.** Soies antérieures. **E**. Soies moyennes. **F.** Soies postérieures. **G.** Acicules antérieures. **H.** Acicules postérieures. Echelle : A, 0,5 mm ; B, C, 0,2 mm ; D-H, 20 µm.

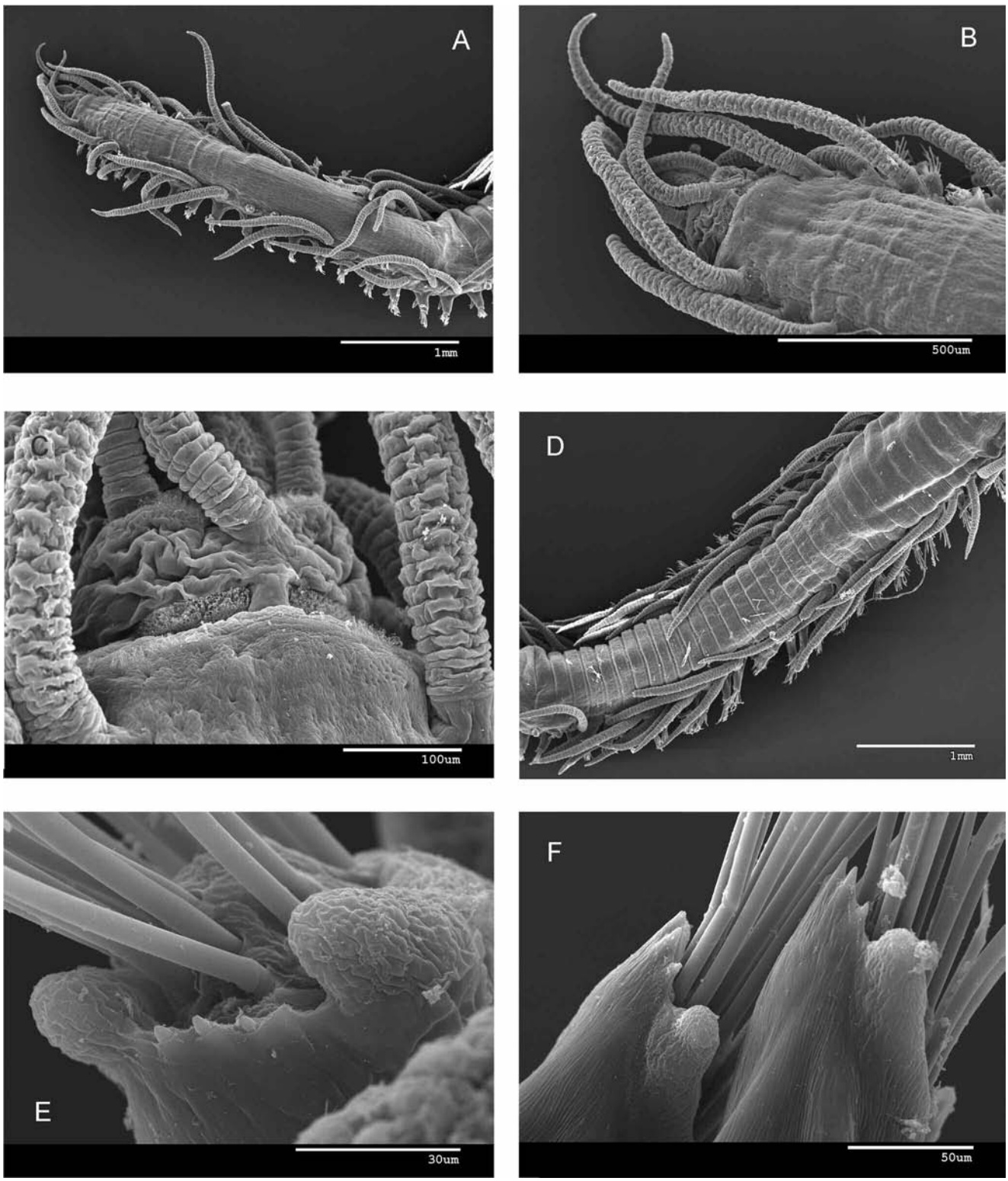

Figure 2. ***Syllis bella*.** SEM. **A, B.** Anterior end, dorsal view. **C.** Prostomium, dorsal view. **D.** Midbody segments. **E, F.** Midbody parapodia, lateral view.

Figure 2. ***Syllis bella*.** MEB. **A, B.** Extrémité antérieure, vue dorsale. **C.** Prostomium, vue dorsale. **D.** Segments moyens. **E, F.** Parapodes moyens, vue latérale.

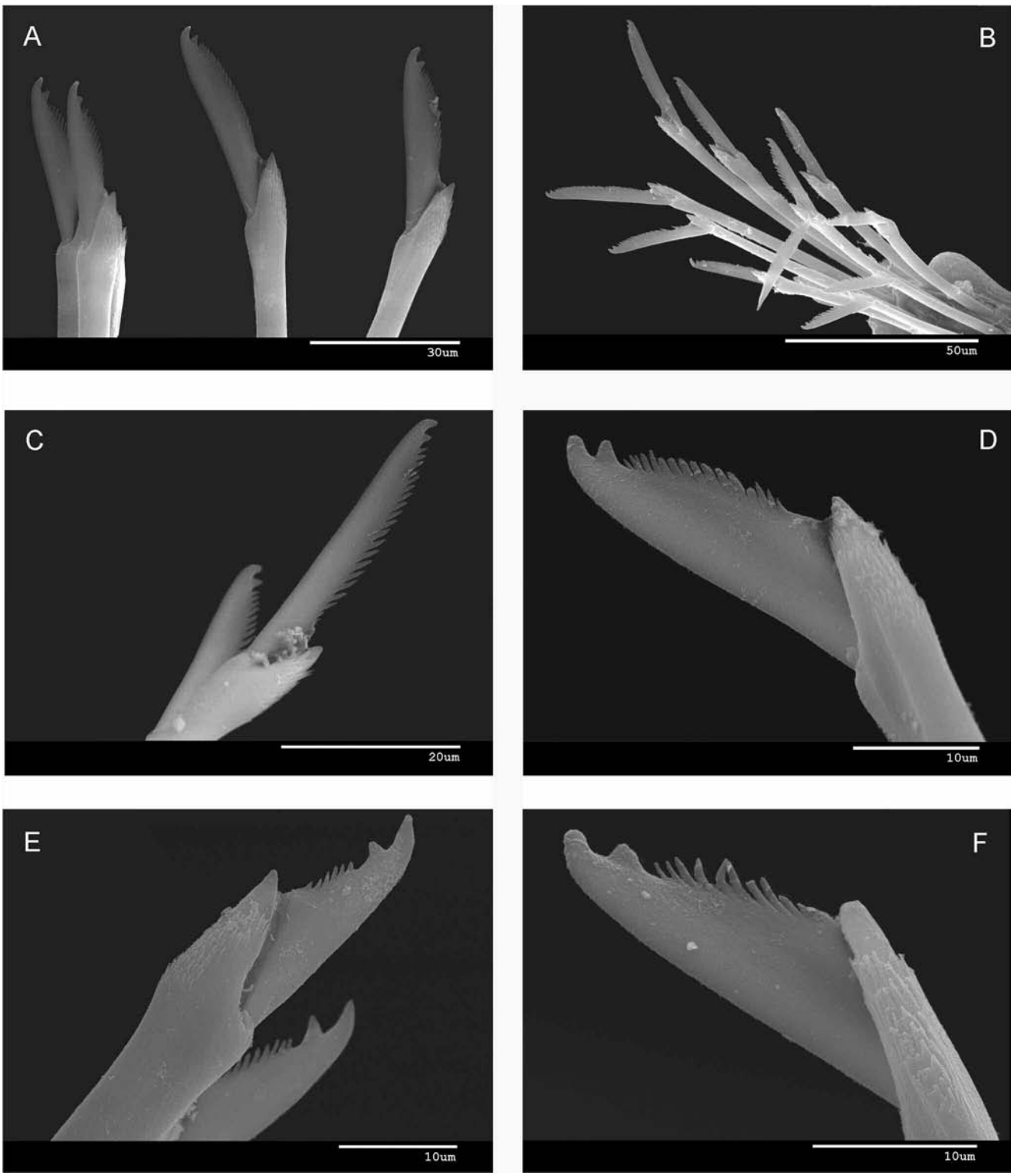

Figure 3. ***Syllis bella*.** SEM. **A-C.** Anterior chaetae. **D.** Midbody chaeta. **E, F.** Posterior chaetae.
Figure 3. ***Syllis bella*.** MEB. **A-C.** Soies antérieures. **D.** Soie moyenne. **E, F.** Soies postérieures.

longitudinal line. Colour pattern more distinct on proventricular segments (Fig. 1A). Prostomium wider than long, with two pairs of eyes in trapezoidal arrangement, anterior ones slightly larger than posterior pair, eye spots absent. Antennae, tentacular and dorsal cirri long and thick, with short, wide articles. Median antenna inserted on middle of prostomium, longer than combined length of prostomium and palps, with 38 articles; lateral antennae shorter, inserted on anterior margin of prostomium, with 27 articles (Fig. 1A). Palps triangular, longer than prostomium, fused at base with a distinct median groove. Nuchal organs forming two ciliary grooves between prostomium and peristomium (Fig. 2C). Peristomium similar in length to subsequent segments. Two pairs of tentacular cirri, dorsal tentacular cirri longer than antennae (Fig. 2B), with 43 articles, ventral ones shorter with 25 articles. Dorsal cirri of most anterior segments with 36-40 articles (Fig. 2A). Midbody and posterior dorsal cirri similar in length to anterior ones (Fig. 2D), with 40 articles. Spiral glands inside articles. Cirrophores distinct. Ventral cirri digitiform, inserted proximally and reaching tips of parapodia (Figs 1B, C). Anterior parapodia with 15 compound chaetae, bidentate blades, slightly decreasing in length (most dorsal c. 25 µm, most ventral c. 22 µm), blade edge with short spines (Figs 1D, 3A-C). Midbody parapodia with 11 compound chaetae, blades bidentate, similar in length to anterior ones (most dorsal c. 22 µm, most ventral c. 20 µm), with short spines on edge (Figs 1E, 3D). Posterior chaetigers with 11-14 compound chaetae, blades bidentate, shorter than those of anterior chaetigers (most dorsal c. 18 µm, most ventral c. 16 µm), and short spines on edge (Figs 1F, 3E, F). Shafts with distal spines. Anterior parapodia with 3-4 pointed aciculae, one slightly bent (Fig. 1G); midbody and posterior parapodia with 2-3 pointed aciculae (Figs 1H, 2E, F). Pygidium conical, with two anal cirri (c. 20 articles). Pharynx longer than proventricle, through 11 segments; tooth on anterior margin. Proventricle extending through 4 segments (Fig. 1A), with about 37 rows of muscular cells.

Remarks

The morphological characters of specimens of *S. bella* from Lebanon agree well with the original and subsequent descriptions of the species (type locality: California) and the comparative material studied from Panamá (Capa et al., 2001). However, the presence of this tropical species from the West Pacific Ocean in the Mediterranean Sea was unexpected since it is only known from Central American Pacific and there is not any intermediate report.

Specimens of *Syllis bella* from Lebanon present some variations in the colour pattern. Some specimens lost it completely; while others present transversal dark-red lines on each segment and, most of them, show a coloration patter consisting in red pigmentation principally distributed in anterior, middle and posterior parts of each segments forming transversal lines (the common coloration pattern of this species). These variations in the studied material could be attributed to the different preservation state of the specimens. There are also some small variations in number of articles of dorsal cirri and number of chaetae per parapodium between specimens from Lebanon and those described by Licher (1999) (from California). Specimens from California showed dorsal cirri with 16-32 articles alternatively, while dorsal cirri in specimens from Lebanon had 36-40 articles. Specimens from California had 9-10 compound chaetae per parapodium, while specimens from Lebanon had 11-15. However, these differences could be attributed to the differences in length between both groups of specimens (specimen described from California with 145 segments, specimen from Lebanon with 56). Therefore, there is not any clear difference between Lebanon specimens and those from Pacific Ocean, and we consider this species could have been introduced from its previous range. Genetic techniques will surely provide us with more information to investigate the identity and origin of this species.

Distribution

Pacific Ocean (California, Panamá). Mediterranean Sea (first report).

Syllis columbretensis (Campoy, 1982)

Typosyllis columbretensis Campoy, 1982: 413.
Syllis columbretensis San Martín, 2003: 443-447, figs 244, 245. Çinar & Ergen, 2003: 780.

Material examined

1 specimen (SMF16391), Beirut harbour, 3-8 m, 2.vi.2000.

Distribution

Atlantic Ocean (Spanish coast). Mediterranean Sea.

Syllis corallicola Verrill, 1900

Syllis (Typosyllis) corallicola Verrill, 1900: 603.
Typosyllis corallicola Licher, 1999: 116-119, fig. 54.
Syllis corallicola San Martín, 2003: 439-443, figs 242, 243. Çinar & Ergen, 2003: 780.

Material examined

1 specimen (SMF16412), Ramkine Island, cave, 5-7 m, 31.5.2000. 1 specimen (SMF16401), Selaata, small caves and overhangs, 3-8 m, 18.10.1999. 2 specimens (SMF16378), Kfar Abida, 7-8 m, 30.v.2000.

Distribution

Caribbean Sea (Bermudas, Antillas, Cuba). Atlantic Ocean (Spanish coasts). Mediterranean Sea.

Syllis ferrani Alós & San Martín, 1987

Syllis ferrani Alós & San Martín, 1987: 35-43, figs 1-5. San Martín, 2003: 390-394, figs 213, 214. Çinar & Ergen, 2003: 782.
Typosyllis ferrani Licher, 1999: 221-223, fig. 93.

Material examined

1 specimen (SMF16344), Ramkine Island, with crust and corals, 13 m, 22.x.1999. 2 specimens (SMF16352), Batroun, encrusted cliff, 9 m, 16.x.1999.

Distribution

Mediterranean Sea.

Syllis garciai (Campoy, 1982)

Langerhansia garciai Campoy, 1982: 386-389, p. 375.
Typosyllis garciai Licher, 1999: 74-75.
Syllis garciai San Martín, 2003: 400-405, figs 219, 220, 221. Çinar & Ergen, 2003: 782-783.

Material examined

1 specimen (SMF16424), Barbara, overhang, 26 m, 8.vi.2000. 2 specimens (SMF16355), Batroun, encrusted cliff, 9 m, 16.x.1999.

Distribution

East Atlantic Ocean (Galicia to Cabo Verde Islands). Caribbean Sea (Cuba, Venezuela). Mediterranean Sea.

Syllis gerlachi (Hartmann-Schröder, 1960)

Typosyllis gerlachi Hartmann-Schröder, 1960: 81-82, pl. 6, figs 43-44. Licher, 1999: 127-129, Fig. 57.
Syllis gerlachi San Martín, 2003: 376-378, figs. 205, 206. Çinar & Ergen, 2003: 783.

Material examined

4 specimens (SMF16371), Kfar Abida, 7-8 m, 30.v.2000. 6 specimens (SMF16356), Batroun, encrusted cliff, 9 m, 16.x.1999.

Distribution

Red Sea. East Atlantic Ocean (Galicia to Cape Verde Islands). Mediterranean Sea.

Syllis gracilis Grube, 1840

Syllis gracilis Grube, 1840: 77. Licher, 1999: 289-291, fig. 10A. San Martín, 2003: 413-416, figs 226, 227. Çinar & Ergen, 2003: 784.

Material examined

2 specimens (SMF16436) and 6 specimens (SMF16397), Beirut harbour, 3-8 m, 2.vi.2000. 1 specimen (SMF16432), Chak el Hatab, cave, 5 m, 4.vi.2000. 2 specimens (SMF16349), Ramkine Island, hardground, 13-14 m, 22.x.1999. 4 specimens (SMF16376), Kfar Abida, 7-8 m, 30.v.2000. 5 specimens (SMF16350), Batroun, encrusted cliff, 9 m, 16.x.1999. 1 specimen (SMF16437), Ramkine Island, hardground, 13-14 m, 22.x.1999. 1 specimen (SMF16386), Selaata, small caves and overhangs, 3-8 m, 18.x.99.

Distribution

Apparently cosmopolitan.

Syllis hyalina Grube, 1863

Typosyllis hyalina Grube, 1863: 45, pl. 4, fig. 8. Licher, 1999: 199-205, fig. 86.
Syllis hyalina San Martín, 2003: 426-429, figs 234, 235. Çinar & Ergen, 2003: 784, 785.

Material examined

10 specimens (SMF16402) and 1 specimen (SMF16387), Selaata, small caves and overhangs, 3-8 m, 18.x.1999. 1 specimen (SMF16430), Dora, on spines of *Stylocidaris affinis*, 50 m, 2.v.2000. 1 specimen (SMF16452), Khaldeh, marina Villamar, with *Caulerpa scalpelliformis*, 1-2 m, 7.vi.2000. 2 specimens (SMF16426), Barbara, overhang, 26 m, 8.vi.2000. 1 specimen (SMF16476), Ramkine Island, with crust and corals, 13m, 22.x.1999. 5 specimens (SMF16374), Kfar Abida, 7-8 m, 30.v.2000. 1 specimen (SMF16383), Ras El Chakaa, cliff, 4-8 m, 19.x.1999. 19 specimens (SMF16395), Beirut harbour, 3-8 m, 2.vi.2000. 2 specimens (SMF16441), Ramkine Island, cave, 5-7 m, 31.v.2000. 19 specimens (SMF16360), Batroun, encrusted cliff, 9 m, 16.x1999.

Distribution

Apparently cosmopolitan.

Syllis* cf. *mayeri Musco & Giangrande, 2005
(Figs 4-6)

(?) *Syllis mayeri* Musco & Giangrande, 2005b: 468-472, figs 1-3.

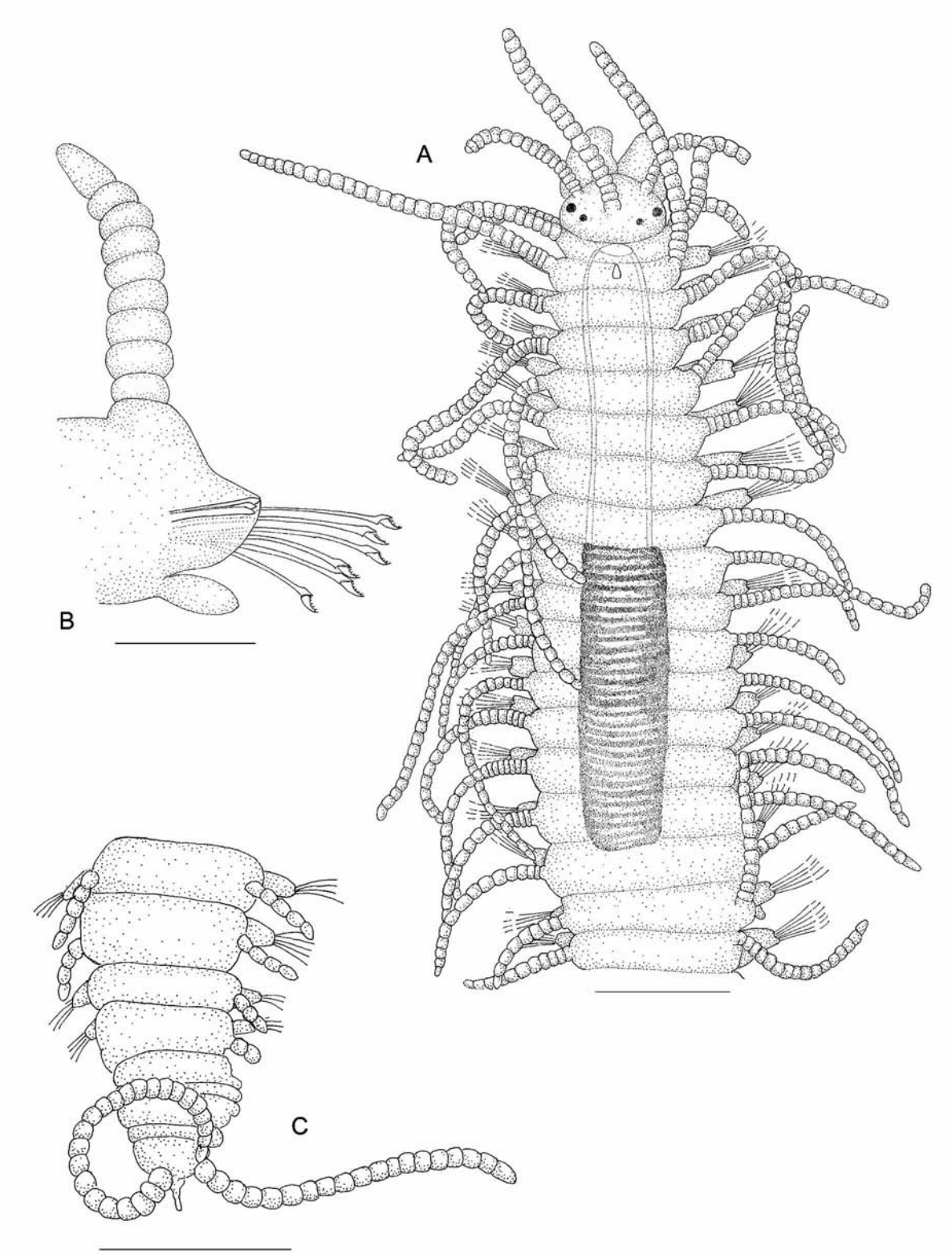

Figure 4. ***Syllis* cf. *mayeri*. A.** Anterior part, dorsal view. **B.** Midbody parapodium, anterior view. **C.** Posterior part, dorsal view. Scale: A, 0.4 mm; B, 98 µm; C, 0.2 mm.

Figure 4. ***Syllis* cf. *mayeri*. A.** Partie antérieure, vue dorsale. **B.** Parapode moyen, vue antérieure. **C.** Partie postérieure, vue dorsale. Echelle : A, 0,4 mm; B, 98 µm; C, 0,2 mm.

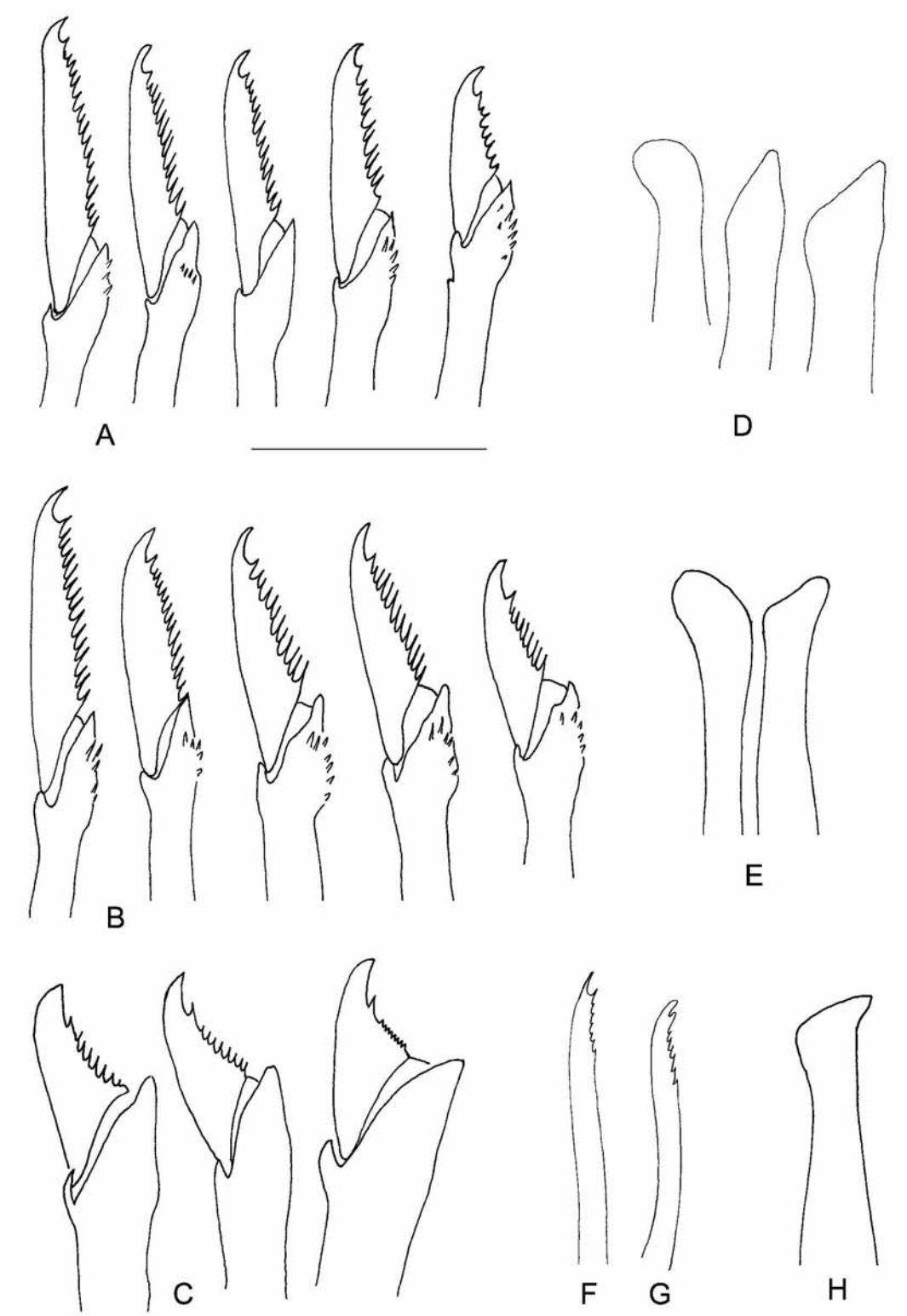

Figure 5. ***Syllis* cf. *mayeri*. A.** Anterior chaetae. **B.** Midbody chaetae. **C.** Posterior chaetae. **D.** Anterior aciculae. **E.** Midbody aciculae. **F.** Dorsal simple chaetae, posterior segment. **G.** Ventral simple chaeta, posterior segment. **H.** Posterior aciculum. Scale: A-H, 20 µm.

Figure 5. ***Syllis* cf. *mayeri*. A.** Soies antérieures. **B.** Soies moyennes. **C.** Soies postérieures. **D.** Acicules antérieures. **E.** Acicules moyens. **F.** Soies simples dorsales, segment postérieur. **G.** Soie simple ventrale, segment postérieur. **H.** Acicule postérieur. Echelle : A-H, 20 µm.

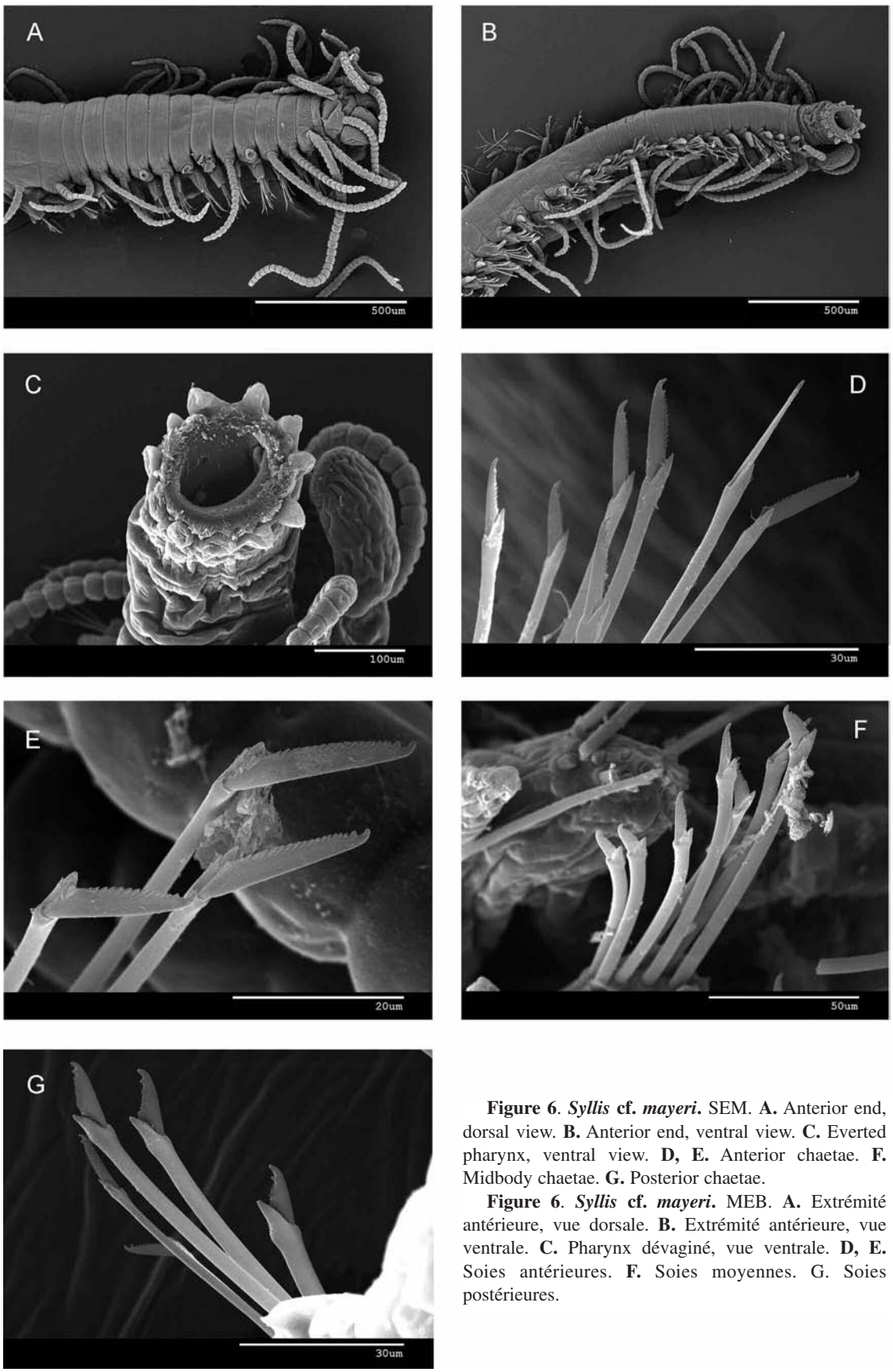

Figure 6. ***Syllis* cf. *mayeri*.** SEM. **A.** Anterior end, dorsal view. **B.** Anterior end, ventral view. **C.** Everted pharynx, ventral view. **D, E.** Anterior chaetae. **F.** Midbody chaetae. **G.** Posterior chaetae.

Figure 6. ***Syllis* cf. *mayeri*.** MEB. **A.** Extrémité antérieure, vue dorsale. **B.** Extrémité antérieure, vue ventrale. **C.** Pharynx dévaginé, vue ventrale. **D, E.** Soies antérieures. **F.** Soies moyennes. G. Soies postérieures.

Material examined

43 specimens (SMF16635), Selaata, small caves and overhangs, 3-8 m, 18.x.1999. 2 specimens (SMF16631), Selaata, caves and overhangs, 23.x.1999. 3 specimens (SMF16634), Jbail, Tablieh, 15-16 m, 17.x.1999. 6 specimens (SMF16469), Ras el Chakaa, cave, 5-6 m, 4.vi.2000. 4 specimens (SMF16630), Barbara, overhang, 26 m, 8.vi.2000. 7 specimens (SMF16629), Ramkine Island, with crust and corals, 13m, 22.x.1999. 29 specimens (SMF16465), Ras El Chakaa, cliff, 4-8 m, 19.x.1999. 1 specimen (SMF16459), Batroun, encrusted cliff, 9 m, 16.x.1999.

Comparative material examined

Syllis mayeri Musco & Giangrande, 2005b. Holotype (MNCN 16.01/10263), Carrie Bow Island (Belize).
Syllis armillaris (Müller, 1771). Several specimens (MNCN 16.01/6744 and 6745), Mediterranean Sea (Types lost).
Syllis gracilis Grube, 1840. 1 syntype (MPW395), Mediterranean Sea. Several specimens (MNCN 16.01/8927, 8928, 8936, 8938, 8948), Mediterranean Sea.
Syllis hyalina Grube, 1863. 1 syntype (MPW396), Lussin Island, Croatia.

Description

Best preserved specimen 8 mm long, 0.7 mm wide, with 70 segments. Prostomium wider than long, with two pairs of eyes in trapezoidal arrangement, anterior ones larger than posterior pair. Median antenna inserted on middle of prostomium, slightly longer than combined length of prostomium and palps, with 20 articles; shorter lateral antennae inserted on anterior margin of prostomium, with 15 articles (Figs 4A, 6A). Palps triangular, similar in length to prostomium, fused at basis with a distinct median groove. Peristomium shorter than subsequent segments, with two pairs of tentacular cirri. Dorsal tentacular cirri similar in length to lateral antennae, with 14 articles, ventral ones with 10 articles (Fig. 4A). Dorsal cirri of most anterior segments with 15-24 articles without a distinct alternation pattern (Fig. 4A). Dorsal cirri after proventricle shorter, with about 10 articles (Fig. 4A & B). Ventral cirri proximally inserted on parapodia, not extending beyond parapodial lobes (Fig. 4B). Anterior parapodia each with 6 compound, heterogomph chaetae, distal part of shafts provided with spines. Bidentate blades, with slight dorsoventral gradation in length (most dorsal c. 25 µm, most ventral c. 13 µm), moderate long spines on the blade edge (Figs 5A, 6D & E). Midbody chaetigers with 6-7 compound chaetae decreasing in number to 4-5 towards posterior segments (Fig. 6G). Blades bidentate, similar to those from anterior blades (Figs 5B & 6F). Posterior chaetae with shorter blades (c. 15-16 µm) (Fig. 5C), distal tips of fangs enlarged. Most posterior chaetigers with one simple dorsal chaeta and one ventral simple chaeta, both bidentate, distally curved and with some subdistal spines (Fig. 5F & G). Anterior parapodia with three aciculae, two distally pointed and one rounded (Fig. 5D). Midbody parapodia with two aciculae, one distally rounded and another distally pointed and slightly curved (Fig. 5E). Posterior segments with one pointed acicula slightly protruding from parapodia (Fig. 5H). Pygidium conical, two anal cirri with 22 articles and a median short anal papilla (Fig. 4C). Pharynx similar in length to proventricle; conical tooth on anterior margin, 10-11 terminal papilla and a distal crown of cilia (Fig. 6B & C). Proventricle extending through 7 segments, with about 40 cell-rows (Fig. 4A). Several specimens developing stolons.

Remarks

The examined specimens are closely related to the species *S. mayeri* from Belize. They are similar in the length and shape of dorsal cirri, which are long and slender on the anterior segments and short and spindle-shaped on the posterior ones. They are also similar in the chaetal shape. Anterior chaetae have in both cases bidentate blades longer than posterior ones, which are short and with distal tips of fangs quite long. Aciculae are similar too in shape and number (Musco & Giangrande, 2005b). Although these similarities are clear, there are also some differences. *Syllis mayeri* has relatively longer anterior dorsal cirri (30-20 articles), but they dismiss in length (7-9 articles) and become spindle-shaped from segments 6-7 towards posterior region. *Syllis* cf. *mayeri* also presents relatively long anterior dorsal cirri (15-24 articles), which dismiss in length becoming shorter and spindle-shaped in the posterior segments (9-10 articles). Notwithstanding, anterior dorsal cirri are shorter than those in *S. mayeri* and they become spindle-shaped and short on the segments after the proventricle (segments 16-17), being present, therefore, in a longer region than they are in *S. mayeri*. The proventricle is similar in length in both species (through 7 segments); however, the pharynx is longer in *S. mayeri* (through 14 segments) than in *S.* cf. *mayeri* (7 segments). In addition, the holotype of *S. mayeri* is considerably larger (24 mm length) while specimens of *S.* cf. *mayeri* from Lebanon are about (7-13 mm length). Considering these differences and the distant geographic distributions (Belize and Mediterranean), studied specimens are identified as *S.* cf. *mayeri*. Only two specimens (holotype and paratype) of *S. mayeri* have been found and, probably, more material of this species would be useful to clarify similarities and differences between both species.

Other similar species are *S. armillaris*, *S. gracilis* and *S. hyalina*, which are considered cosmopolitan species.

However, material from different parts of the world of same species often present some variations in chaetae shape and/or cirri length, being possible that they are in fact different taxa. All these species could actually be complexes of species, and therefore, there would be necessary a more detailed comparative study of material around the world to distinguish populations or even possible different species, which are currently blurred under the same name.

Distribution

Mediterranean Sea.

Syllis jorgei San Martín & López, 2000

Syllis jorgei San Martín & López, 2000: 430. San Martín, 2003: 382-386, figs 208-210. Çinar & Ergen, 2003: 785.

Material examined

1 specimen (SMF16409), Ramkine Island, cave, 5-7 m, 31.v.2000. 1 specimen (SMF16370), Kfar Abida, 7-8 m, 30.v.2000.

Distribution

Atlantic Ocean (Canary Islands). Mediterranean Sea.

Syllis prolifera Krohn, 1852

Syllis prolifera Krohn, 1852: 66-75, pl. 3, fig. 1. San Martín, 2003: 344-347, figs 186, 187. Çinar & Ergen, 2003: 786-787.
Typosyllis prolifera Licher, 1999: 135-140, figs 17S, 5B.

Material examined

1 specimen (SMF16393), Beirut harbour, 3-8 m, 2.vi.2000.

Distribution

Apparently cosmopolitan.

Syllis pulvinata (Langerhans, 1881)

Typosyllis pulvinata Langerhans, 1881: 97-98, 104. Licher, 1999: 158-160, fig. 70.
Syllis pulvinata San Martín, 2003: 372-375, figs 202-204. Çinar & Ergen, 2003: 787.

Material examined

2 specimens (SMF16431), El Zahrani, Harf el Hawieh el Jouani, 14 m, 6.vi.2000. 1 specimen (SMF16427), Barbara, overhang, 26 m, 8.vi.2000.

Distribution

East Atlantic Ocean (Gulf of Biscay to Canary Islands). Red Sea. Mediterranean Sea.

Syllis variegata Grube, 1860

Syllis variegata Grube, 1860: 85-86, pl.3, fig. 6. San Martín, 2003: 351-354, figs 190, 191. Çinar & Ergen, 2003: 788.
Typosyllis variegata Licher, 1999: 101-108, figs 10B, 17D, 49.

Material examined

1 specimen (SMF16368), Batroun, encrusted cliff, 9 m, 16.x.1999.

Distribution

Apparently cosmopolitan.

Trypanosyllis aeolis Langerhans, 1879

Trypanosyllis aeolis Langerhans, 1879: 558. San Martín, 2003: 315-319, figs 174-176. Çinar & Ergen, 2003: 789.

Material examined

1 specimen (SMF16453), Khaldeh, marina Villamar, with *Caulerpa scalpelliformis*, 1-2 m, 7.vi.2000.

Distribution

Apparently circumtropical.

Trypanosyllis zebra (Grube, 1860)

Syllis zebra Grube, 1860: 86. Licher, 1999: 295, 296. San Martín, 2003: 311-315, figs 171-173. Çinar & Ergen, 2003: 789-790.

Material examined

2 specimens (SMF16414), Ramkine Island, cave, 5-7 m, 31.v.2000. 5 specimens (SMF16404), Selaata, small caves and overhangs, 3-8 m, 18.x.1999. 1 specimen (SMF16377), Kfar Abida, 7-8 m, 30.v.2000. 1 specimen (SMF16382), Ras El Chakaa, cliff, 4-8 m, 19.x.1999. 1 specimen (SMF16394), Beirut harbour, 3-8 m, 2.vi.2000. 3 specimens (SMF16366), Batroun, encrusted cliff, 9 m, 16.x.1999. 1 specimen (SMF16442) Jabail, Tablieh, 15-16 m, 17.x.1999.

Distribution

Apparently cosmopolitan.

Discussion

Until present, several species of syllids have been considered introduced in the Mediterranean Sea. For instance, *Paraexogone wolfi* San Martín, 1991 (from Gulf of México and Florida) and *Sphaerosyllis longipapillata*

Hartmann-Schröder, 1979 (from Eastern Australia) were found in Northern Cyprus by Çinar et al. (2003), and *Eusyllis kupffferi* (from Madeira, Cuba and Canary Islands) by Çinar & Ergen 2003. The species *Branchiosyllis exilis* and *Opisthosyllis brunnea* (Ergen et al., 2002) had been traditionally considered Lessepsian migrants; however, Ergen et al. (2002) suggested that they could not be considered real Lessepsian species since their distribution is very wide. *Streptosyllis arenae* Webster & Benedict, 1884 was proposed by Zenetos et al. (2005) as a possible alien species, although its identification is still not certain. In contrast, *S. longipapillata* was proposed as a real Lessepsian migrant (Çinar et al., 2003). Likely, this number of Lessepsian migrants and, in general, the number of all introduced species is very low, and many other species may possibly remain unreported (Çinar, 2003a).

Detecting new aliens depends on accurate taxonomic identifications and the knowledge of local biodiversity (Çinar et al., 2005). However, the lack of knowledge on this issue is, effectively, one of the principal problems in understanding patterns of syllid distribution (Çinar & Ergen, 2002; 2003; Çinar et al., 2003; Musco & Giangrande, 2005a). Another problem is the possible existence of complexes of species, whose identity is blurred under one common specific name; some examples are: *B. exilis*, *S. armillaris*, *S. hyalina* and *S. gracilis* (Martin & Britayev, 1998; San Martín, 2003; Musco & Giangrande, 2005b). Besides, updating of syllid inventories is obviously necessary if aiming to detect possible migrations (Musco & Giangrande, 2005a). Thus, these set of difficulties usually make the identification of introduced species, and the explanation of possible paths of migration, gather in a scenario of unstable conjectures. However, our knowledge of the group is rapidly increasing, and all the small contributions we are currently undertaking shall surely provide a more robust theoretical rationale upon which to identify the origins of the polychaete fauna in the Mediterranean Sea, as well as of other areas.

There are several possibilities that might explain the ways of introduction of the two new reports for the Mediterranean described herein. *Exogone breviantennata* has a circumtropical geographical distribution. The presence of this species on the Lebanon coast and its absence in other well-studied basins of the Mediterranean suggest that it is a newly introduced species for the Mediterranean. It was also reported in the Red Sea (as *E. ovalis*, a synonymy). Hence, the establishment in habitats of the Lebanon utilizing the pathway of the Suez Canal cannot be counter-argued, and therefore, it could be considered as a possible Lessepsian migration. Its possible occurrence on other Levant coasts should notwithstanding be re-checked. In contrast, *S. bella* presents a quite distant distribution from the Mediterranean (Eastern Central Pacific Ocean), and its presence in the Mediterranean coasts is more difficult to explain. We postulate that probably this species could have migrated by fouled ships. The maritime traffic is quite abundant between all seas and it is responsible, in many cases, of the introduction of maritime foreign species (Stigzelius et al., 1997; Çinar & Ergen, 2005; Çinar et al., 2005 & 2006). Musco & Giangrande (2005a) suggested the possibility of a general "tropicalization" trend of the Mediterranean fauna. This has been advocated as a possible explanation for the current presence of several species otherwise typical from warm waters. In turn, other species, generally from cold waters, previously reported in the Mediterranean, are seemingly absent now since they have not been recently reported. The presence of *E. breviantennata* and *S. bella* could support this hypothesis.

Finally, the geographic distribution of *Syllis mayeri* is less known. It has only been reported in a distant area, such as Belice (Musco & Giangrande, 2005b). If the identification of *S.* cf. *mayeri* would finally be corroborated as *S. mayeri*, the pathway by which it has become established in waters of the Lebanon would be unknown at this stage.

Acknowledgments

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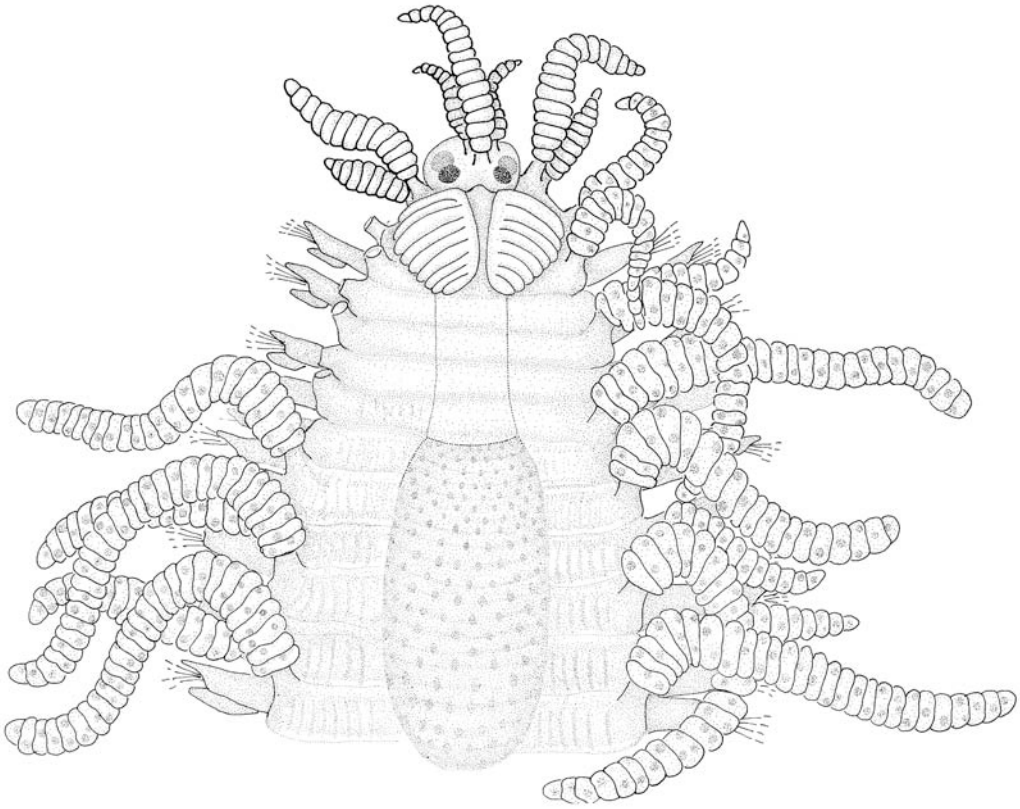
BLOQUE II

REVISIÓN DE GÉNEROS DE LA FAMILIA SYLLIDAE



1. Re-description of some enigmatic genera of Syllidae (Phyllodocida: Annelida). Aguado, M.T. & San Martín, G. In press. *Journal of Marine Biological Association of United Kingdom*.

RE-DESCRIPTION OF SOME ENIGMATIC GENERA OF SYLLIDAE (PHYLLODOCIDA: POLYCHAETA)

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ABSTRACT

Several type series of unusual and poorly known genera of Syllidae have been examined. New diagnoses for the following genera: *Anguillosyllis* Day, 1963, *Clavisyllis* Knox, 1957, *Lamellisyllis* Day, 1960 and *Nuchalosyllis* Rullier & Amoureux, 1979, and re-descriptions of their type species are provided. *Brachysyllis* Imajima & Hartman, 1964, previously synonymized with *Dioplosyllis* Gidholm, 1962, is herein considered to be a valid taxon. The species *Brachysyllis infuscata* Ehlers, 1901 is also re-described. Three genera are considered to be non-valid taxa: *Braniella* Hartman, 1964, synonymous with *Anguillosyllis*; *Alluaudella* Gravier, 1905, synonymous with *Odontosyllis* Claparède, 1863 and *Exogonella* Hartmann, 1961, synonymous with *Parexogone* Mesnil & Caullery, 1918. Their type species are herein re-described and assigned to their corresponding valid genus. Finally, *Exogonoides* Day, 1963 is considered *nomina dubia* since its relationships with other syllids could not be established. Keys to species of *Anguillosyllis* and *Brachysyllis* are also included.

Key words. Redescription, synonymies, key to species, generic diagnoses.

INTRODUCTION

The family Syllidae is one of the most diverse families of Polychaeta; according to San Martín (2003) the family has more than 50 genera and 700 valid species, although in recent years this number has rapidly increased with the discovery of new genera and species (San Martín, 2002, 2005; San Martín & López, 2003; San Martín & Hutchings,

2006; San Martín *et al.*, 2007). Syllidae are currently divided into four subfamilies: Syllinae Grube, 1850; Exogoninae Langerhans, 1879; Eusyllinae Malaquin, 1893; and Autolytinae Langerhans, 1879. These subfamilies were diagnosed based on a few characteristics. For example, Exogoninae are characterized by having totally or partially fused palps, one or two pairs of tentacular cirri, and short smooth dorsal cirri; Autolytinae by having nuchal epaulettes and the absence of ventral cirri; Syllinae by having articulated antennae and dorsal cirri; Eusyllinae by having smooth or pseudoarticulated antennae and dorsal cirri. Reproductive modes were also taken into account in the separation of these subfamilies; Eusyllinae and Exogoninae are mostly epigamic, while Syllinae and Autolytinae are mostly schizogamic (San Martín, 2003).

Notwithstanding the above, several authors have considered that the subfamilies within Syllidae could have been created solely for practical reasons, and some of them might not represent true monophyletic groups (Fauchald, 1977; Nygren, 1999; Nygren and Sundberg, 2003; Glasby, 2000; Pleijel, 2001; San Martín, 2003). In addition, the separation between these subfamilies is based only on very few features, and in several cases the reproductive mode is unknown. Furthermore, several features are common between subfamilies.

Currently, we are involved in a global revision of the family Syllidae within the scope of a global phylogenetic scenario. For this purpose it is necessary to establish whether genera are valid or in fact conflictive in taxonomic terms. In this context, the main objective of the present study is to revise the type series of intriguing genera with features unique to their family, and/or showing a mixture of features that define several subfamilies. These puzzling genera are *Alluaudella* Gravier, 1905, *Anguillosyllis* Day, 1963, *Brachysyllis* Imajima & Hartman, 1964, *Braniella* Hartman, 1964, *Clavisyllis* Knox, 1957, *Exogonella* Hartmann, 1961, *Exogonoides* Day, 1963, *Lamellisyllis* Day, 1960 and *Nuchalosyllis* Rullier & Amoureux, 1979. All these genera have been revised; some are re-described accepting their taxonomic status, whereas others are synonymized with other genera.

MATERIAL AND METHODS

Material examined is located at different institutions. Some specimens were studied during visits to the Museum National d'Histoire Naturelle, Paris (MNHN), the Museum für Naturkunde der Humboldt-Universität, Berlin (ZMB), and the Zoologisches Institut und Zoologisches Museum, Universität Hamburg (ZMH). Other specimens were taken on loan from different institutions, such as the Natural History Museum of London (NHML), The Smithsonian Institution (USNM), the Natural History Museum of Los Angeles County (NHMLAC), the South African Museum, Cape Town (SAM), the National Institute of Water and Atmosphere Research, New Zealand (NIWA) and the Universidad de La Laguna, Tenerife, Canary Islands (UL), and later examined at the Universidad Autónoma de Madrid (UAM).

Examinations were made using stereomicroscopes and optical microscopes provided by the respective institutions. Drawings were made to scale, with a camera lucida drawing tube attached to each optical microscope. The studied specimen of *Clavisyllis alternata* Knox, 1957 was critical point dried and subsequently coated with 102 Å of gold and examined under Philips XL30 electronic microscope, connected to an EDAX DX4i analyser at SIDI (Servicio Interdepartamental de Investigación, UAM). One segment of *Brachysyllis infuscata* (Ehlers, 1901) was critical point dried and then coated with 80% of gold and 20% of palladium and examined using a LEO 1450 VP electronic microscope at the ZMB. The width of specimens was measured at the level of proventricle, excluding parapodia.

Most studied material were holotypes, these were old and fragile and, unfortunately, it proved impossible to distinguish several features due to the poor state of preservation, in these cases the information provided by the original descriptions was taken into account. In addition to this, dissection of certain holotypes proved impossible due to the unique nature of the material.

RESULTS

SYSTEMATICS

Genus *Anguillosyllis* Day, 1963

Anguillosyllis Day, 1963: 400.

Braniella Hartman, 1965: 72-73.

Diagnosis

Body small, meiofaunal. Prostomium with three small antennae and two palps; palps elongated, fused, with a distal notch, more or less marked. Without eyes. One pair of papilliform tentacular cirri. Antennae and tentacular cirri minute, papilliform. Dorsal cirri long, filiform, coiled over dorsum. Ventral cirri present, digitiform, inserted medially to distally. Parapodia relatively long, triangular, with a short prechaetal and elongated postchaetal lobe. Compound chaetae heterogomph, with elongated, slender blades. Pharyngeal tooth absent. Proventricle barrel-shaped.

Type species

Anguillosyllis capensis Day, 1963.

Remarks

Day (1963) placed *Anguillosyllis* within the subfamily Exogoninae because of the complete fusion of palps and the presence of a single pair of tentacular cirri (a common feature in several Exogoninae genera). Day (1967) and later, Böggemann & Purschke (2005) maintained this genus within Exogoninae. However, *Anguillosyllis* is far from being a typical Exogoninae, since it lacks a pharyngeal tooth and the dorsal cirri are long and filiform; common features in several Eusyllinae species. However, the fusion of palps and the presence of minute, papilliform antennae and a single pair of tentacular cirri are diagnostic of this subfamily. Unfortunately, its reproductive mode is totally unknown. This information would be extremely useful in order to determine the relationships of this

genus with other Syllidae. Strictly, *Anguillosyllis* has intermediate morphological characteristics between Exogoninae and Eusyllinae.

The genus *Braniella* Hartman, 1964 has the same diagnosis as *Anguillosyllis*: fused palps (at least for more than half of their lengths), papilliform antennae, a single pair of small tentacular cirri, long and smooth dorsal cirri, digitiform ventral cirri (medially to distally inserted on parapodia), enlarged parapodial lobes, compound heterogomph chaetae and also the absence of a pharyngeal tooth. Therefore, *Braniella* is considered herein synonymous with *Anguillosyllis*.

All the known species of this genus live in the deep sea (183-5500 m). The elongated postchaetal lobes are quite translucent, with fine walls, likely acting as branchiae.

Key to species

1. Palps fused only on basal half. Posterior parapodial lobe short, similar in shape and length to anterior lobe. Dorsal cirri on chaetiger 2 present. *Anguillosyllis palpata*
- Palps fused almost all their lengths. Posterior parapodial lobes elongated, distinctly longer than anterior lobes. 2
2. Palps relatively short and broad, fused all along their lengths. Postchaetal lobes triangular. Ventral cirri proximally to medially inserted on parapodia, digitiform. Dorsal cirri on chaetiger 2 absent. *Anguillosyllis pupa*
- Palps elongated, triangular, with a distal notch. Postchaetal lobes digitiform, distinctly long. Ventral cirri short, papilliform, almost distally inserted on parapodia. Dorsal cirri on chaetiger 2 present. *Anguillosyllis capensis*

Anguillosyllis capensis Day, 1963

(Figure 1)

Anguillosyllis capensis Day, 1963: 400-401, fig. 5a-d. Day, 1967: 271, fig. 12.10z-zzz. Böggemann & Purschke, 2005: 222-223, fig.1.

Material examined

Holotype NHML 1963.1.29, Agulhas Bank, South Africa, 34º 51'S 28º 4'E, 183 m, sand.

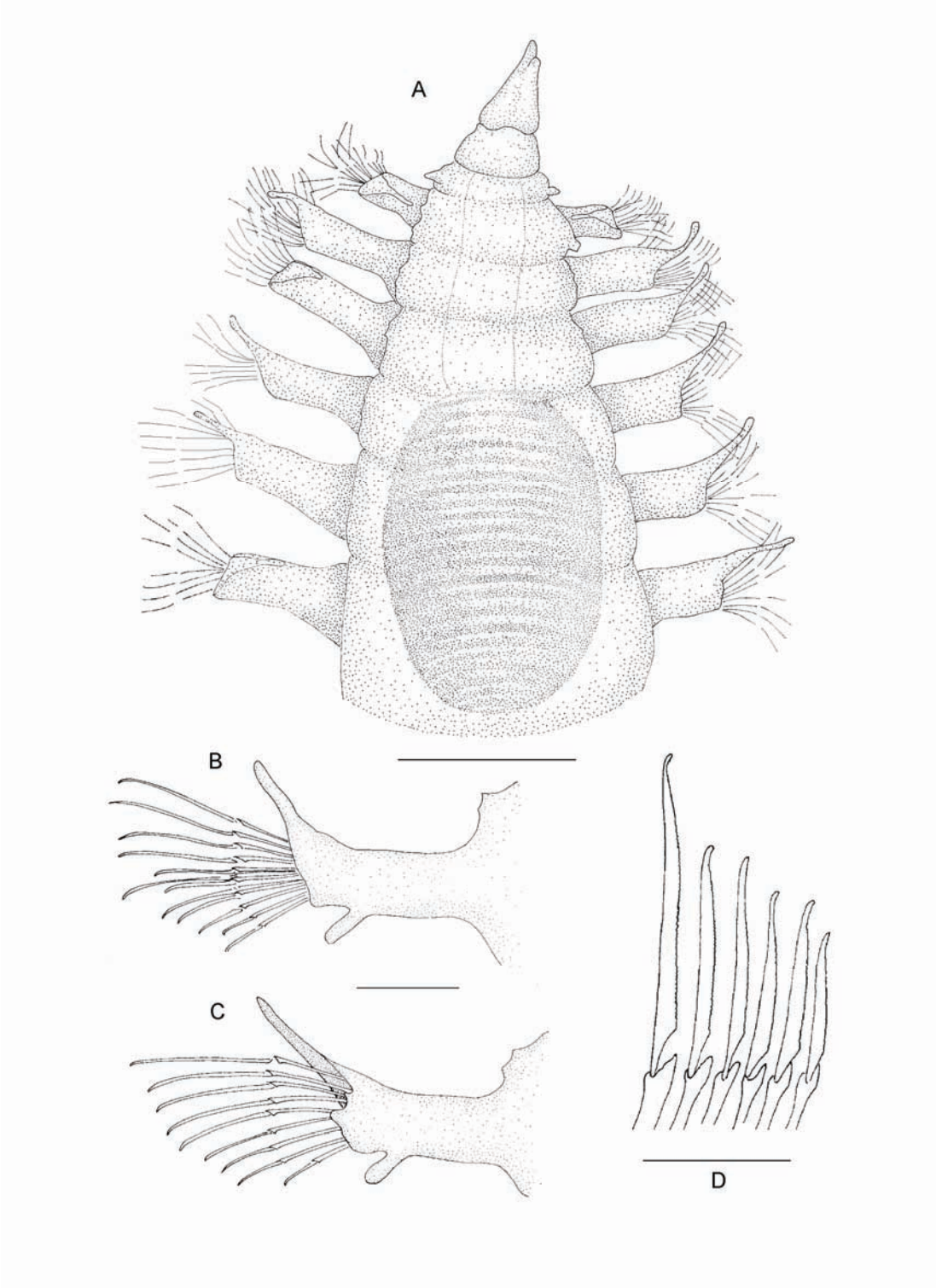

Figure 1. *Anguillosyllis capensis*. Holotype. (A) Anterior end, dorsal view; (B) Midbody parapodium, posterior view; (C) Midbody parapodium, anterior view; (D) Midbody chaetae. Scale bars A, 0.4 mm; B, C, 98 m; D, 48 m.

Description

Holotype incomplete; antennae, tentacular and dorsal cirri detached, 1.5 mm long, 0.7 mm wide, with 6 segments. No sign of pigmentation. Prostomium oval, broader than long. Palps tapered, longer than prostomium, fused for over half of their length, one of them without distal end (Fig. 1A). Eyes absent. Antennae lost (three club-shaped antennae, *fide* Day, 1963). Peristomium shorter than subsequent segments, with a pair of tentacular cirri, papilliform (Fig. 1A). Segments becoming wider towards posterior end, more than twice as broad as long in last segments. All dorsal cirri lost (long and slender, without any sign of annulation, often twisted and coiled, *fide* Day, 1963). Ventral cirri digitiform, inserted distally on parapodia, not reaching parapodial lobes (Figs 1B, C). Parapodia with one long, triangular posterior lobe (Fig. 1B) (retractile, *fide* Day, 1963) and short, papilliform anterior lobe (Fig. 1C). Numerous compound, heterogomph chaetae per parapodium, with long and slender blades, unidentate, decreasing in length from dorsal (98 ! m) to ventral (48 ! m), with minute and fine spines on cutting edge of blades (Fig. 1D). Shafts smooth. Aciculae not visible by transparency. Pharynx though 4 segments (with 6 distal papillae, *fide* Day, 1963). Pharyngeal tooth absent. Proventricle broad, barrel-shaped, through 3 segments, and about 25-30 muscle cell-rows.

Remarks

Böggemann & Purschke (2005) found several specimens of this species in the Angola basin and they could distinguish 1-4 aciculae within parapodia (with pointed tips) and 9-10 distal pharyngeal papillae. They also described a pair of smooth anal cirri similar in length and shape to dorsal cirri and one additional median anal papilla. This species has been found at depths between 183 and 5449 m.

Distribution

Cape Agulhas, South Africa and Angola Basin, Angola.

Anguillosyllis pupa (Hartman, 1965) n. comb.

(Figure 2)

Braniella pupa Hartman, 1965: 72-73, pl. 8. Hartman & Fauchald, 1971: 51.

Material examined

1 spec. ZMH P-13585, off New England, 400-500 m. 1 spec. USMN 103505, North Atlantic Ocean, USA, Georges Bank, Northern Slope.

Description

Holotype complete, 1.5 mm long, 0.4 mm wide, with 10 segments. Body broad with tapering ends, no signs of colour pattern. Prostomium broader than long. Antennae papilliform (median one detached). Palps triangular, longer than proventricle, completely fused, with dorsal groove. Eyes absent. Three short papilliform antennae inserted in a straight row on posterior half of prostomium (Fig. 2A). Peristomium shorter than subsequent segments, with one pair of short, papilliform tentacular cirri, smaller than antennae (Fig. 2A). Dorsal cirri smooth, long and coiled, most of them detached. Dorsal cirri on chaetiger 2 absent (*fide* Hartman, 1965). Ventral cirri digitiform, medially inserted on parapodia, not reaching level of tips of parapodial lobes. One long, triangular posterior lobe (Fig. 2B). Numerous compound, heterogomph chaetae per parapodium. Dorsal blades long, pseudospinigers (95 ! m), decreasing in length to ventral falcigers, falciger like (10 ! m), all unidentate (Fig. 2C). Fine and short spines on cutting edge of blades. Shafts smooth. Pygidium conical, with two anal cirri and distal cilia (*fide* Hartman, 1965). Pharynx through 4 segments without pharyngeal tooth. Distal papillae on pharynx not observed. Proventricle almost spherical, through 3 segments, with about 20-25 muscle cell rows.

Remarks

Hartman (1965) did not describe the fine spines along the cutting edge of the blades. This species has been found at depths between 400 and 4892 m.

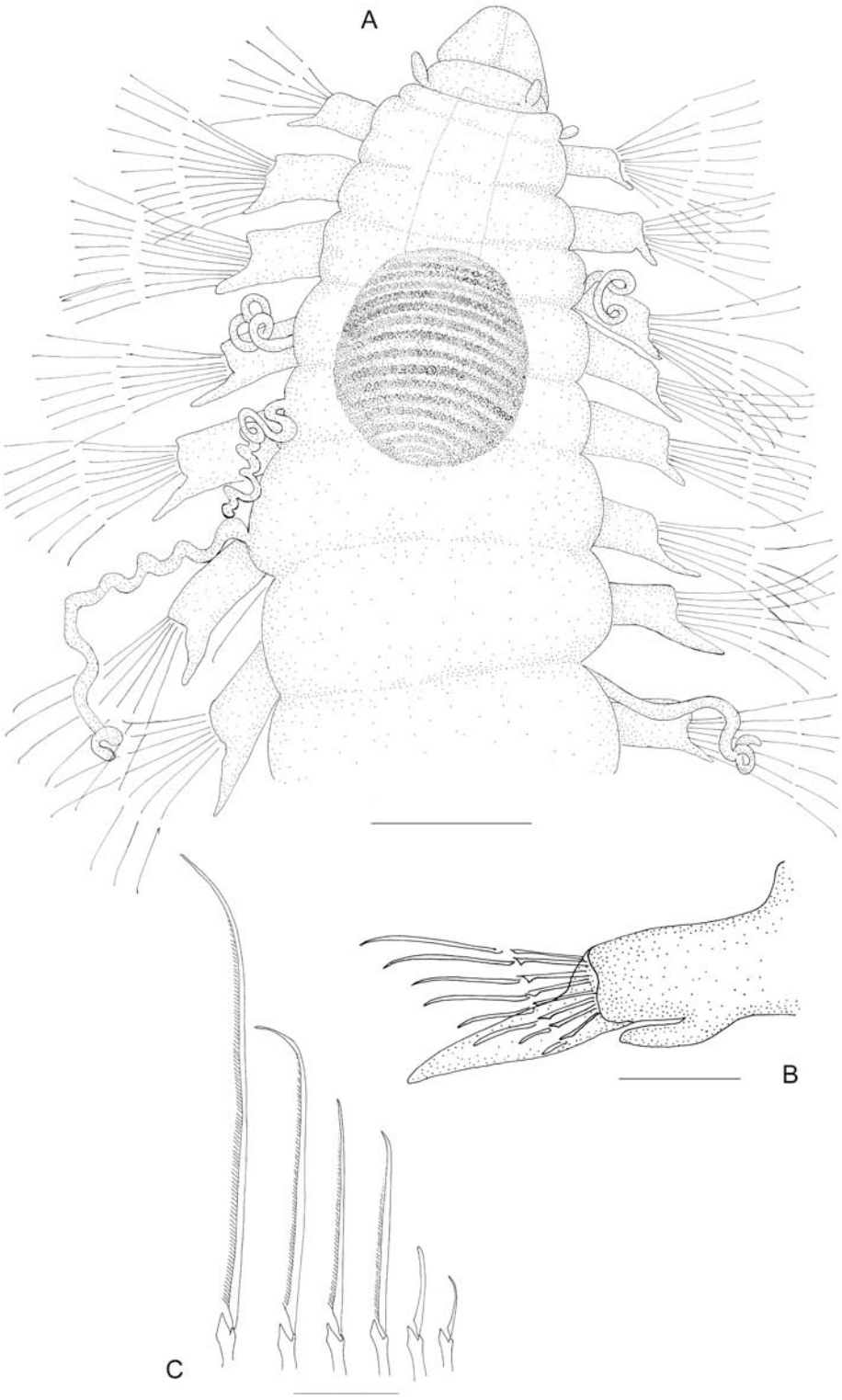

Figure 2. *Anguillosyllis pupa* n. comb. P.13585. (A) Anterior end, dorsal view; (B) Midbody parapodium, anterior view; (C) Midbody chaetae. Scale bars A, 0.2 mm; B, 74 ! m; C, 20 ! m.

Distribution

Off New England, Northeastern South America.

Anguillosyllis palpata (Hartman, 1967) n. comb.

Braniella palpata Hartman, 1967: 55, pl. 14.

Material examined

1 spec. ZMH P-24133, Antarctic Ocean, Weddell Sea.

Remarks

Anguillosyllis palpata has long triangular palps fused at their basal half, papilliform antennae and only one pair of papilliform tentacular cirri. Ventral cirri are medially inserted to parapodia. Anterior and posterior parapodial lobes are present. The pharyngeal tooth is absent. The species was well described and illustrated by Hartman (1967). Found at depths between 383 and 3770 m.

Distribution

Antarctic Ocean and nearby areas (Cape Horn, Drake Passage, Weddell Sea).

Genus *Brachysyllis* Imajima & Hartman, 1964

Brachysyllis Imajima & Hartman, 1964:108.

Diagnosis

Body large, macrofaunal, with 13 chaetigers plus a pre-anal achaetous segment. Segments more or less trapezoidal. Palps long, free at bases, with a subdistal small papilla. Prostomium with four eyes. Nuchal organs as ciliary rows. Rows of transversal cilia covering dorsum and ventrum. Antennae, and tentacular, anal and dorsal cirri long, filiform and smooth. Ventral cirri long, filiform, inserted proximally to parapodia. Parapodia elongate, with a triangular pre-chaetal lobe, dorsally located. Compound

chaetae falcigerous, blades bidentate, dorsal and ventral simple chaetae absent. Aciculae bending distally. Pharynx wide, straight, with a large anterior dorsal tooth and an incomplete ventral arc of small denticles (5-6), surrounded by a crown of distal pharyngeal papillae. Proventricle rectangular, shorter than pharynx. Reproduction by epigamy.

Type species

Brachysyllis japonica Imajima & Hartman, 1964.

Remarks

Imajima & Hartman (1964) described *Brachysyllis* as a new genus and *B. japonica* as the type species. They assigned the previously described species *Amblyosyllis infuscata* Ehlers, 1901 to this genus. Later, *Brachysyllis* was synonymized with *Dioplosyllis* Gidholm, 1962 by Imajima (1966). Mueller & Fauchald (1976) presented a table with features of the 4 species tentatively belonging to *Dioplosyllis*: *D. cirrosa* Gidholm, 1962, *D. infuscata*, *D. japonica* and *D. broadi* Mueller & Fauchald, 1976. Afterwards, *D. broadi* was considered synonymous with *D. lagunae* (Hartman, 1961) by Kudenov & Harris (1995) and Perkins (1981) described a new species of this genus, *D. octodentata* Perkins, 1981. Another species described as *Dioplosyllis* (*D. tridentata* Kudenov & Harris, 1995) does not agree with the diagnosis of this genus and will be assigned to another genus in a future work.

However, we consider that there are enough differences to maintain *Brachysyllis* and *Dioplosyllis* as two different genera since the 5 species, until the moment belonging to *Dioplosyllis*, can be easily divided into two clear groups. The first group includes the species *B. infuscata*, *B. japonica* and *D. lagunae*, which have a short body, with a fixed number of chaetigers (13 in all known species) plus one achaetous, pre-anal segment; segments more or less trapezoidal; palps totally free at bases, with a subdistal papilla; ventral cirri long, filiform and proximally located on parapodia; and numerous aciculae (around 5), which are distally acute and curved (Imajima & Hartman, 1964; Mueller & Fauchald, 1976). The second group includes *D. cirrosa* and *D. octodentata*, which have a long body, with numerous rectangular segments (50-63), without pre-anal achaetous

segment, palps fused at bases without subdistal papillae, ventral cirri short, digitiform, distally inserted and 1-2 aciculae distally truncated (Gidholm, 1962; Perkins, 1981). The type series of *D. cirrosa* has been lost, but we have examined specimens identified as *D. octodentata* from the Canary Islands (Núñez & San Martín, 1992) and have been able to check these differences. In addition to the morphological differences, the first group apparently has a distribution restricted to the Pacific Ocean (*B. infuscata* in Chile; *B. japonica* in Japan; and *B. lagunae* in California), and the second group is only known from the Atlanctic Ocean (*D. cirrosa* in NE Atlantic and Mediterranean; *D. octodentata* in the Gulf of México, and the Canary Islands). Consequently, we consider *Brachysyllis* as a valid taxon, including *B. japonica, B. infuscata,* and *B. lagunae* and *Dioplosyllis* only comprising two species: *D. cirrosa* and *D. octodentata*.

Nevertheless, both genera appear to be closely related, since they share similar shape of palps, segments and ciliated parapodia, very long, filiform dorsal cirri, and significantly a very similar pharyngeal armature. Other genera with similar pharyngeal armature (a middorsal tooth and a ventral arc of denticles) are *Eusyllis* Malmgren, 1867, and *Miscellania* Martín, Alós & Sardá, 1990. *Miscellania* is much smaller, meiofaunal, it has antennae with distal swelling, and its dorsal cirri are small, similar to those of the Exogoninae. *Eusyllis* has shorter dorsal cirri, pseudoarticulated in some species, with numerous denticles on the pharyngeal rim and the ventral cirri are short and digitiform (San Martín, 2003).

Brachysyllis is similar to *Amblyosyllis* in having the long dorsal cirri, often coiled over the dorsum, invariable number of chaetigers, with a pre-anal achaetous segment, segments more or less trapezoidal, and the presence of an elongated parapodial lobe. However, *Brachysyllis* is different in the pharyngeal armature (*Amblyosyllis* possesses a complete trepan, though lacks a middorsal tooth and a crown of soft papillae), ventral cirri (short, triangular in *Amblyosyllis*) and the absence of nuchal epaulettes. Besides, *Amblyosyllis* has a long and coiled pharynx, while *Brachysyllis* likely has a straight pharynx. The latter character could not be observed since the dissection of the holotype was not possible.

The three previously described *Brachysyllis* species seem to be very similar to each other and could be synonyms. Coming to a reliable conclusion would require the re-

examination of types of these species together with a detailed study of new, well-preserved material.

Key to species

1. Pharyngeal armature composed by a ventral arc with 6 small teeth and one large tooth dorsally located. *B. japonica*
- Pharyngeal armature composed by a ventral arc with 5 small teeth and one large tooth dorsally located. 2
2. Compound chaetae bidentate with distal and proximal teeth large and rounded, both similar in size. *B. lagunae*
- Compound chaetae bidentate with proximal tooth pointed, distal tooth larger than proximal one. *B. infuscata*

Brachysyllis infuscata (Ehlers, 1901)

(Figures 3, 4)

Amblyosyllis infuscata Ehlers, 1901a: 258-259. Ehlers, 1901b: 100-102, pl. 11, figs. 4-9. Augener, 1922: 188-189.

Brachysyllis infuscata Imajima & Hartman, 1964: 110.

Dioplosyllis infuscata Mueller & Fauchald, 1976: 21 (table).

Material examined

Holotype ZMB 6742, Juan Fernández, Chile, 36.5 m.

Description

Holotype incomplete, fragmented in several pieces, anterior fragment with 6 segments, 4.5 mm long, 1.5 mm wide. 14 segments, 15.5 mm long (whole body length and segments *fide* Ehlers, 1901b). Body fragile; greyish brown. Segments trapezoidal, with transversal, pigmented grooves with clumps of cilia, also present in parapodia (Fig. 3A, 4B-D). Prostomium oval, with 4 eyes in trapezoidal arrangement difficult to distinguish (Fig. 3A). Antennae lost, lateral ones inserted on anterior margin of prostomium, median

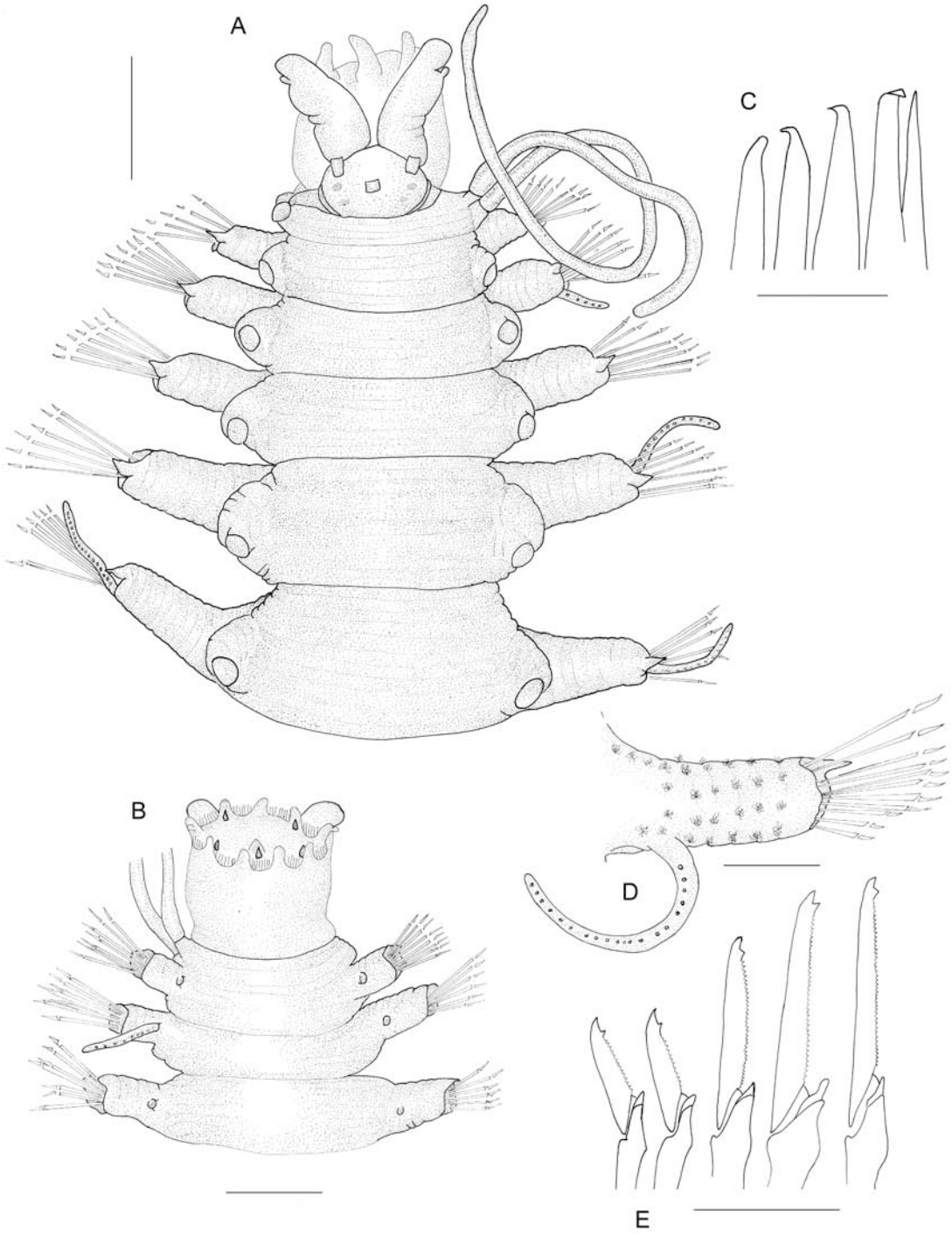

Figure 3. *Brachysyllis infuscata*. (A) Anterior end, dorsal view; (B) Everted pharynx, ventral view; (C) Midbody aciculae; (D) Midbody parapodium, posterior view; (E) Midbody falcigers. Scale bars A, B, 0.7 mm; C, E, 50 ! m; D, 0.3 mm.

inserted in the middle of prostomium, between anterior pair of eyes. Palps completely free, divergent, ventrally folded, twice as long as prostomium, with one small lateral papillae on subdistal end (Fig. 3A). Peristomium shorter than subsequent segments, with 2 pairs of smooth, long tentacular cirri (only present on one side), dorsal one longer than ventral. Most of dorsal cirri lacking, present ones very long, as long as 5-6 segments (Fig. 3A), smooth with small granular material inside. Parapodial lobes long, half midbody segment width, conical in shape, with conical prechaetal lobe, distally pointed and postchaetal lobe shorter and distally truncate (Fig. 3D). Ventral cirri long, digitiform, inserted on proximal half of parapodia, with orange granular material inside (Fig. 3D, 4A), nearly twice as long as parapodia. Parapodia with about 20 compound, heterogomph chaetae, blades distinctly bidentate, with short spines on cutting edge of blades (Figs 3E, 4E-H). Within fascicle, blades decreasing in length from dorsal (88 ! m) to ventral (42 ! m). Distal part of fangs with two tips (Fig. 3E). Five straight aciculae per parapodia, some ending in a thin tip bending distally (Fig. 3C). Pygidium lost. Pharynx shape not visible. Several crowns of structures on anterior part of the pharynx; a crown of ten distal papillae, a crown of large cilia and five internal conical teeth (Fig. 3B). Pharyngeal tooth not clearly observed (large and conical *fide* Ehlers, 1901b, pl. 11, fig. 7). Proventricle extending through 2 segments, with about 50-60 muscle cell rows.

Remarks

The species was described with only one large middorsal pharyngeal tooth (Ehlers, 1901b), but later Augener (1922) described it with an additional incomplete arc of 5 small teeth. The pharyngeal opening also exhibits a crown of long cilia, not previously described. Another characteristic not previously described is the presence of transverse grooves with clumps of cilia along the body surface. Nuchal organs could not be studied since they are a difficult characteristic to observe in preserved material; however, the absence of nuchal epaulettes was noted. Other species of the genus were described with nuchal organs on ciliary ridges (Mueller & Fauchald, 1976). These ciliary ridges are probably grooves, more evaginated than usual in syllids, otherwise, the presence of nuchal organs on ridges would be a unique characteristic in Syllidae.

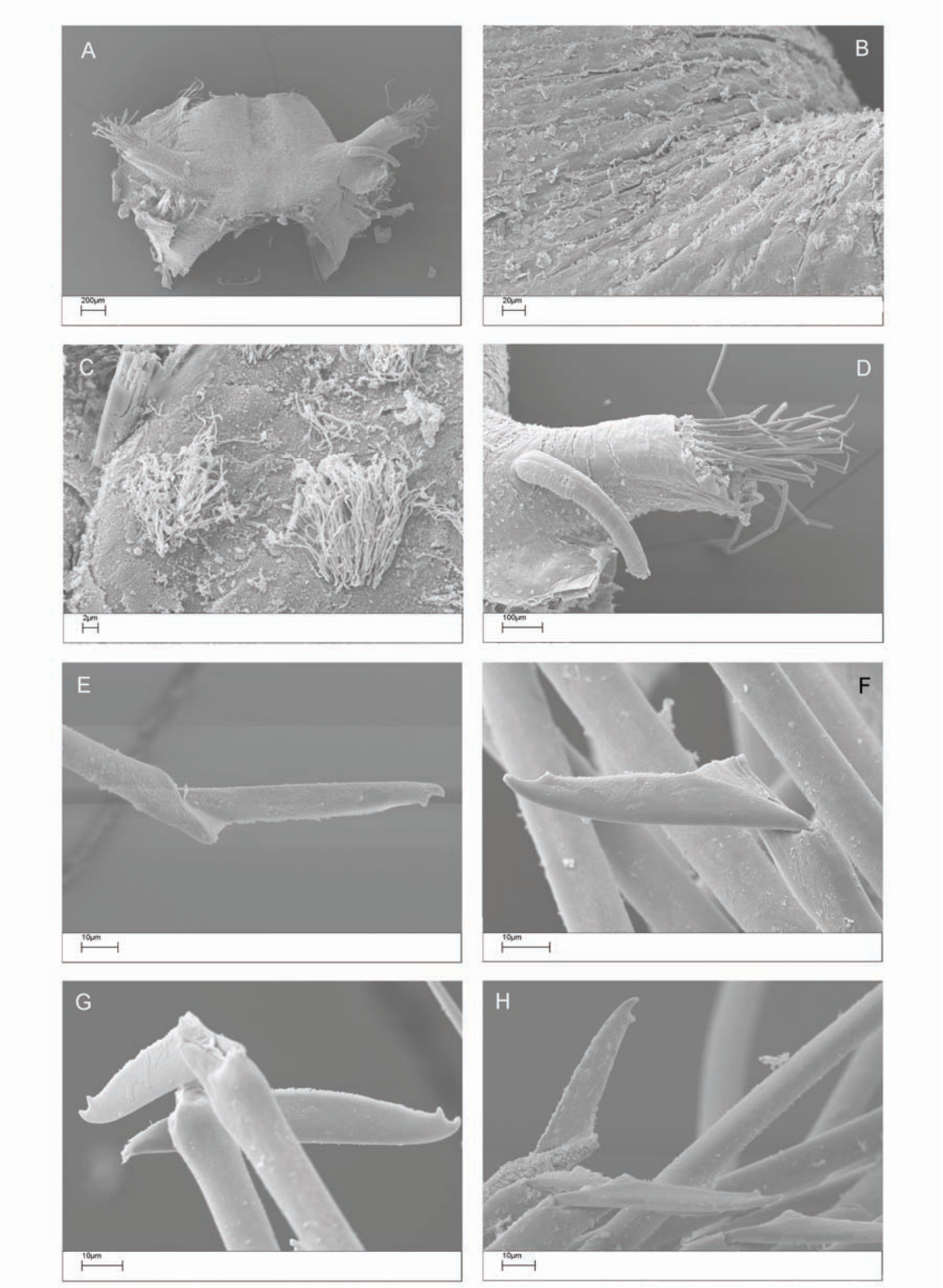

Figure 4. *Brachysyllis infuscata*. SEM. (A) Midbody segment, ventral view; (B) Body surface, midbody segment; (C) Clumps of cilia, midbody segment; (D) Midbody parapodium; (E-H) Midbody falcigers.

Distribution

Juan Fernández, Chile.

Genus *Clavisyllis* Knox, 1957

Clavisyllis Knox, 1957: 493.

Diagnosis

A macrofaunal species, body long, thick. Prostomium with four eyes, three antennae and two palps. Palps fused at base, ventrally directed. Peristomium with two pairs of tentacular cirri. Two prominent, long, sinuous nuchal epaulettes, together with single, digitiform nuchal cirrus. Antennae, tentacular and dorsal cirri large, ovoid, inflated, with distinct cirrophores; ventral cirri ovoid. Compound heterogomph falcigers with blades having long spines on cutting edges. Pharynx and proventricle of similar length; anterior margin of pharynx with a mid dorsal tooth and a crown of soft papillae. Proventricle barrel-shaped.

Type species

Clavisyllis alternata Knox, 1957. Type series lost.

Remarks

Knox (1957) could not assign this genus to any subfamily. He found some similarities with Exogoninae in terms of the shape of cirri and with Autolytinae given the presence of nuchal epaulettes. The genus also has some common features with *Amblyosyllis* (currently located within Eusyllinae) and *Lamellisyllis*, such as the presence of parapodial lobes and nuchal epaulettes. The presence of single nuchal cirri between nuchal epaulettes is unique in Syllidae. Only one species is known from this genus, *Clavisyllis alternata*. The holotype has been lost and there is only one specimen identified as *Clavisyllis alternata*.

Clavisyllis alternata Knox, 1957

(Figures 5, 6)

Clavisyllis alternata Knox, 1957: 493-496, figs.1-3.

Material examined

1 spec. NIWA 4067, New Zealand, North Island, Port of New Plymouth, 39º09'18"S; 174º05'70"E, 8 m, 17/04/2002.

Description

Specimen complete, 13 mm long, 1 mm wide, fragmented, with 61 segments. Live specimen orange, eyes red (*fide* Knox, 1957). Preserved specimen with whitish body, brownish parapodia and dorsal cirri. Body strongly arched, broad, tapering posteriorly. Prostomium rounded, with two pairs of large, oval eyes, in a trapezoidal arrangement; posterior pair slightly larger than anterior ones (Fig. 5A). Palps ventrally folded (Fig. 5B), fused at their base, as long as prostomium. Antennae, tentacular and dorsal cirri with cylindrical ceratophores or cirrophores and distal, ovoid and inflated ceratostyles or cirrostyles, respectively (Figs 5A. 6A, B). Ceratostyles and cirrostyles with a reticulate surface (Figs 6B, E). Lateral antennae inserted on anterior end of prostomium, median antenna inserted on middle of prostomium, between posterior pair of eyes (Figs 5A, 6A, B). Nuchal epaulettes arising from posterior end of prostomium, sinuous and long, attached through their length to dorsum, reaching to chaetiger 8, with rows of cilia on lateral side and clumps of cilia covering dorsal side (Figs 5A, 6A-D). A short, digitiform nuchal cirrus present between nuchal epaulettes, inserted on posterior end of prostomium, reaching chaetiger 2 (Fig. 5A). Peristomium shorter than subsequent segments, covered by nuchal epaulettes; difficult to see dorsally. Two pairs of tentacular cirri, dorsal pair larger than ventral ones. Dorsal cirri similar to dorsal tentacular cirri, alternating in their point of insertion and size over dorsum (Fig. 5A). Dorsal cirri more dorsally inserted and smaller than those inserted more laterally (Fig. 5A). Ventral cirri conical, not reaching tips of parapodial lobes (Fig. 5D). Parapodia with a large stout rounded lobe projecting dorsally to chaetal bundle (Fig. 5D). About 30 compound, heterogomph chaetae per parapodium. Anterior and posterior blades short (29-32 ! m), bidentate, both teeth similar

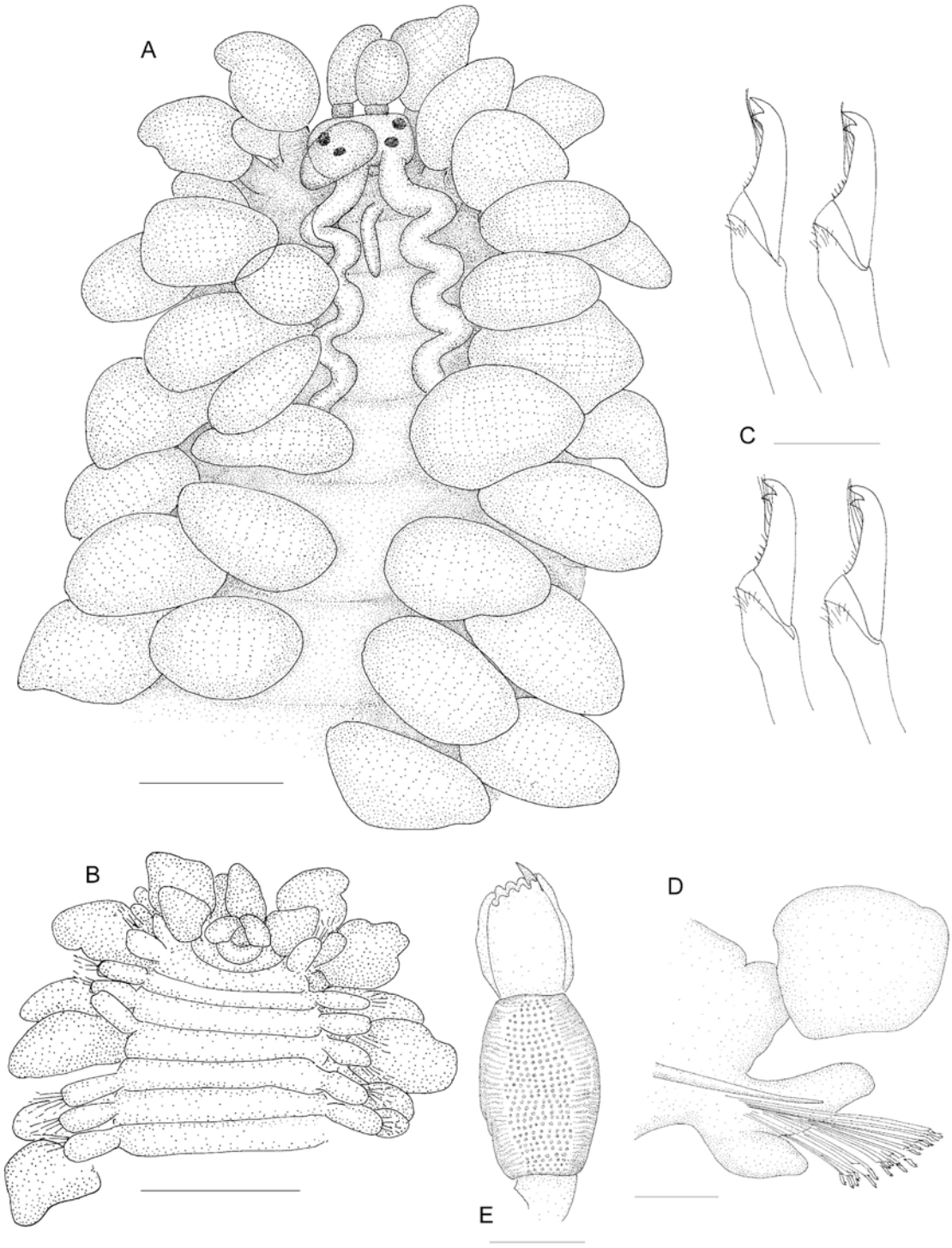

Figure 5. *Clavisyllis alternata*. (A) Anterior end, dorsal view; (B) Anterior end, ventral view; (C) Midbody falcigers; (D) Midbody parapodium, anterior view; E. Pharynx and proventricle. Scale bars A, 0.4 mm; B, 0.8 mm; C, 20 ! m; D, 0.2 mm; E, 0.5 mm.

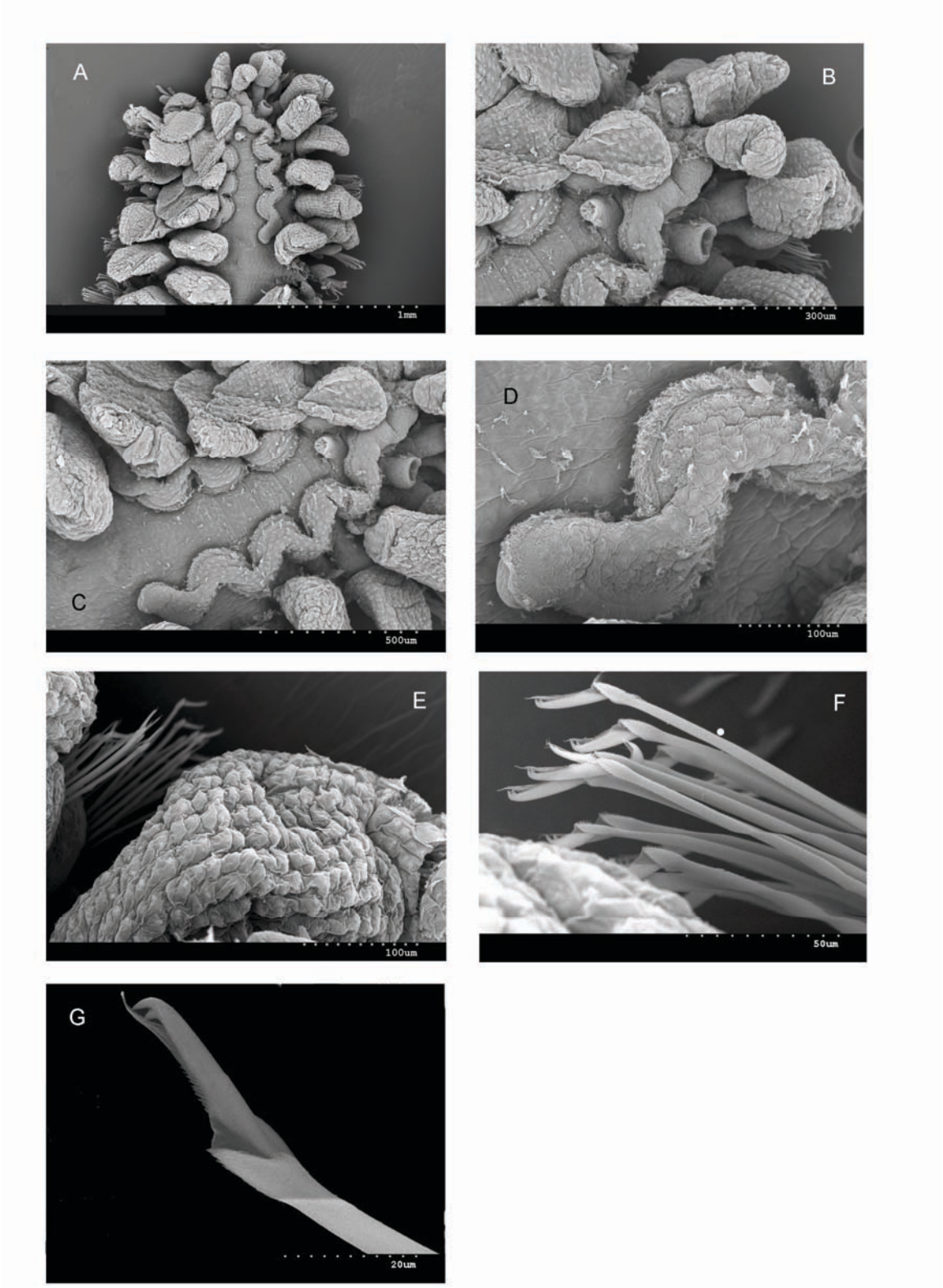

Figure 6. *Clavisyllis alternata*. SEM. (A, B) Anterior end, dorsal view. (C, D) Nuchal epaulettes; (E) Dorsal cirrus, midbody chaetiger; (F, G) Midbody falcigers.

in size and length; short spines basally on cutting edge; long spines distally surpassing

distal teeth (Figs 5C, 6F, G). One acicula per parapodia, straight and distally pointed (Fig. 5D). Dorsal and simple chaetae not seen. Pygidium conical with two anal cirri similar to dorsal cirri. Pharynx straight, shorter than proventricle, with 10 distal papillae and a pharyngeal tooth long and conical, anteriorly located (Fig. 5E). Proventricle through 3 segments, with about 45 muscle cell rows.

Distribution

New Zealand (North Island, Port of New Plymouth and type locality: Menzis Bay, Banks Peninsula on *Sertularia*).

Genus *Lamellisyllis* Day, 1960

Lamellisyllis Day, 1960: 319.

Diagnosis

A macrofaunal species, body long, thick. Prostomium with four eyes, three lamella-shaped or foliaceous antennae and two palps fused at base. Two pairs of tentacular cirri, dorsal pair foliaceous, ventral pair cirriform. Two prominent nuchal epaulettes. Dorsal cirri large, ovoid and foliaceous, with distinct cirrophores; ventral cirri ovoid. Compound heterogomph falcigers with blades having long spines on cutting edge. Pharynx longer than proventricle. Proventricle barrel-shaped.

Type species

Lamellisyllis comans Day, 1960.

Remarks

Although Day (1960, 1967) considered that there was only one pair of tentacular cirri, the re-examination of type material revealed that there are in fact two pairs of tentacular cirri on peristomium. The genus was previously placed within Autolytinae because of the presence of nuchal epaulettes, although it was suggested that there could be a subfamily for this genus together with *Clavisyllis* (Day, 1960). The only known species of this

genus, *Lamellisyllis comans*, presents similarities with *Clavisyllis alternata*. Both species have unusual dorsal cirri, foliaceous in *Lamellisyllis* and inflated in *Clavisyllis*, nuchal epaulettes and developed parapodial lobes. These latter two features are also present in *Amblyosyllis*. Members of Autolytinae, in general, also have nuchal epaulettes. The holotype has eggs within posterior segments (see below) and this evidence could suggest that this species reproduces itself epigamically. If the reproductive mode could be confirmed, it would suggest a closer relationship with Eusyllinae rather than Autolytinae. The genus has only one species, with one specimen.

Lamellisyllis comans Day, 1960

(Figure 7)

Lamellisyllis comans Day, 1960: 319, fig. 7f-i. Day, 1967: 257.

Material examined

Holotype SAM A20924. False Bay, South Africa, 8-12 m.

Description

Holotype complete, 8 mm long, 1 mm wide, with 50 segments. Body pale, dorso-ventrally flattened, with tapering ends. Prostomium dorsally covered by dorsal tentacular cirri, rounded, wider than long. Four eyes in rectangular arrangement, all similar in size (Fig. 7A). Palps triangular, longer than prostomium, fused at base (Fig. 7B). Three foliaceous antennae, lateral pair arising from anterior margin of prostomium, median one inserted on middle of prostomium (Fig. 7A). Two grooved, finger-like nuchal organs diverging from posterior margin of prostomium towards laterals of chaetiger 3 (Fig. 7A). Peristomium with two pairs of tentacular cirri, dorsal ones foliaceous, dorsally covering prostomium and peristomium, ventral ones with cylindrical cirrophore and digitiform cirrostyle (Fig. 7B). Dorsal cirri foliaceous and flattened, oval to circular (Figs 7A, H). Ventral cirri conical, exceeding length of parapodial lobes (Fig. 7H). Parapodia with a triangular, dorsal parapodial lobe distally located (Fig. 7H). Parapodia with about 20

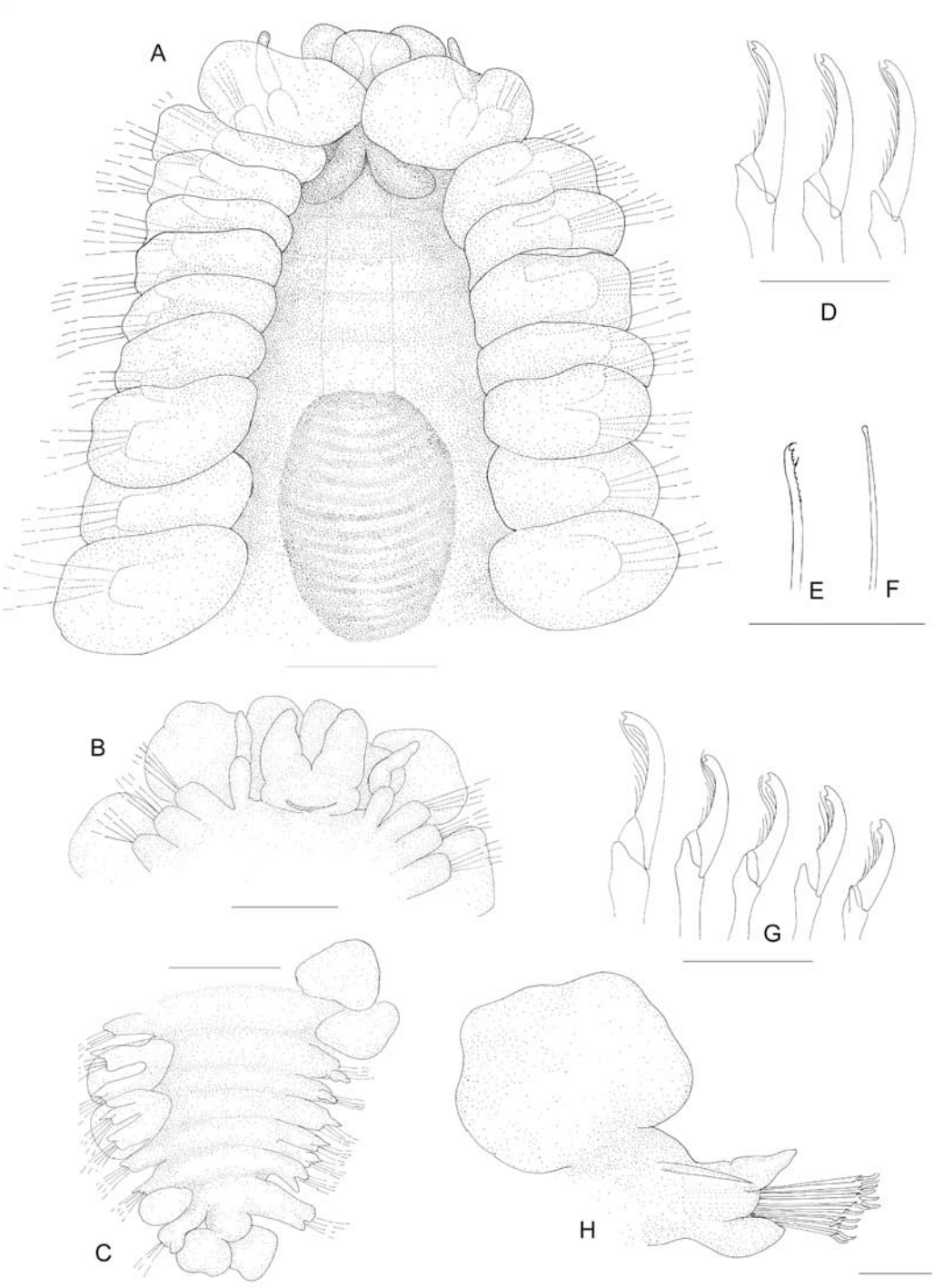

Figure 7. *Lamellisyllis comans*. (A) Anterior end, dorsal view; (B) Anterior end, ventral view; (C) Posterior end, dorsal view; (D) Anterior falcigers; (E) Dorsal simple chaeta, posterior parapodium; (F) Ventral simple chaeta, posterior parapodium; (G) Posterior falcigers; (H) Midbody parapodium, anterior view. Scale bars A, C, 0.5 mm; B, H, 0.4 mm; D-G, 48 ! m.

compound, heterogomph chaetae, decreasing in number and size towards posterior part of body. Blades bidentate, both teeth similar in size and length, long spines on edge, distal ones long, reaching distal teeth (Figs 7D, G). Anterior blades all similar in length (63 ! m) posterior ones decreasing in length on the fascicle from dorsal blades (60 ! m) to ventral ones (37 ! m). Single acicula per parapodium, straight and distally pointed (Fig. 7H). Posterior parapodia with one dorsal simple chaeta, unidentate, distally rounded (Fig. 7F), and one ventral simple chaeta bidentate, with distal tooth longer than proximal one; with spines subdistally, with one larger spine (Fig. 7E). Pygidium rounded with two anal cirri foliaceous, smaller than dorsal cirri (Fig. 7C). Pharynx straight, through 6 segments (Fig. 7A). Distal papillae and pharyngeal tooth not observed (one anterior dorsal tooth *fide* Day, 1960). Proventricle barrel-shaped, through 3-4 segments (Fig. 7A), with about 20 muscle cell rows. Female holotype with numerous oocytes within body.

Distribution

False Bay, South Africa.

Genus *Nuchalosyllis* Rullier & Amoureux, 1979

Nuchalosyllis Rullier & Amoureux, 1979: 164.

Diagnosis

Body long, ribbon shaped, with numerous segments. Prostomium with two pairs of eyes and three antennae anteriorly located. Palps triangular, fused at base. Two pairs of tentacular cirri. Antennae, tentacular, dorsal and anal cirri distinctly articulated. A pair of prominent nuchal epaulettes, with several transversal lamellae. Parapodia conical, with enlarged, triangular prechaetal lobes. Ventral cirri conical, exceeding parapodial lobe. Compound chaetae, heterogomph falcigers. Pharynx with a large anterior dorsal tooth and a crown of 10 distal pharyngeal papillae. Reproduction by schizogamy.

Type species

Nuchalosyllis lamellicornis Rullier & Amoureux, 1979.

Remarks

Nuchalosyllis has a feature that makes it different to any other genera of Syllidae; the comb-like shape of the nuchal epaulettes. Nuchal epaulettes are typical in most of the genera of Autolytinae (which lack ventral cirri) but they are also present in *Amblyosyllis*, *Clavisyllis* and *Lamellisyllis*, the former currently located within Eusyllinae and the latter two with uncertain position; all of them with distinct ventral cirri. *Nuchalosyllis* may be related to these species, however their epaulettes are unique (with several lamellae) and its reproduction is schizogamic. The reproductive mode could suggest that the species may well belong to or may well be related to the subfamily Syllinae. *Nuchalosyllis lamellicornis* closely resembles *Trypanosyllis* in having numerous segments and a ribbon-like body. However, *Nuchalosyllis* does not possesses a trepan, characteristic feature of *Trypanosyllis*, and its nuchal organs are markedly different. The genus has only one species, with one specimen.

Nuchalosyllis lamellicornis Rullier & Amoureux, 1979

(Figure 8)

Nuchalosyllis lamellicornis Rullier & Amoureux, 1979: 164-166, fig. 6.

Material examined

Holotype MNHN 1302, Brazil, near Salvador, 44-60 m, sand with stones and broken shells.

Description

Holotype fragmented, anterior part 27 mm long, 1.8 mm wide with 125 segments and posterior part 22 mm long and 124 segments; stolon developing on posterior end (Fig. 8F). Body dorso-ventrally flattened, pale yellow to orange without colour markings. Cirrophores markedly pigmented in orange. Antennae and tentacular cirri weakly pigmented in pale yellow. Dorsal cirri with bright yellow to orange granular material inside (Fig. 8A). Transversal grooves and crests on dorsal surface of midbody segments

towards posterior ones. Prostomium oval, slightly wider than long; two pairs of dark reddish eyes in open trapezoidal arrangement; anterior pair larger than posterior ones. Median antenna emerging from anterior part of prostomium, between anterior pair of eyes, with relatively short ceratophore and 15 articles. Lateral antennae inserted anteriorly to median one in the middle of prostomium with short ceratophores, shorter than median antenna with 10 articles (Fig. 8A). Palps conical, similar in length to prostomium, free or very basally fused, ventrally folded and not visible dorsally. Large nuchal epaulettes, arising from posterior end of prostomium, with about 7-8 transversal lamellae (Fig. 8A). Peristomium relatively short, with an anterior lobe covering posterior part of prostomium. Two pairs of tentacular cirri; cirrophores well developed, dorsal pair with about 15 articles, ventral pair shorter, with about 10 articles. Anterior and midbody dorsal cirri thick, originating on distinct cirrophores, alternately long and short. Long dorsal cirri longer than body width; with about 20-30 articles; inserted dorso-laterally. Short dorsal cirri with about 15 articles, inserted more ventrally than long cirri (Fig. 8A, E). Posterior dorsal cirri similar to anterior ones but shorter, with about 10-15 articles (Fig. 8F). Ventral cirri lanceolate, anterior ones longer than parapodial lobes, slightly decreasing in length towards posterior segments. Parapodia conical, with a long triangular to digitiform prechaetal lobe inserted on dorsal position and one smaller, oval postchaetal lobe ventrally inserted (Fig. 8F). Anterior parapodia with 12-15 compound falciger chaetae. Blades unidentate, smooth or with small, short, thin spines on cutting edge of blades, 24 ! m long (Fig. 8B). Posterior parapodia with 10 falcigers similar in shape and length to anterior ones. Dorsal and ventral simple chaetae not observed. Three straight and pointed aciculae per parapodia (Fig. 8C). Pharynx through 7 segments, proventricle through six segments, with about 30 muscle cell rows (Fig. 8A). Pharyngeal tooth located on anterior part of pharynx, large and conical, surrounded by a crown of ten papillae. Pygidium in regeneration, conical, without anal cirri (Fig. 9F).

Stolon

Sexual reproduction by stolons formed by posterior budding, stolon beginning on chaetiger 290. Fully developed stolon complete with 37 chaetigers (Fig. 8F). Attachment of stolon to parental specimen directly on dorsal surface, parental specimen ventrally

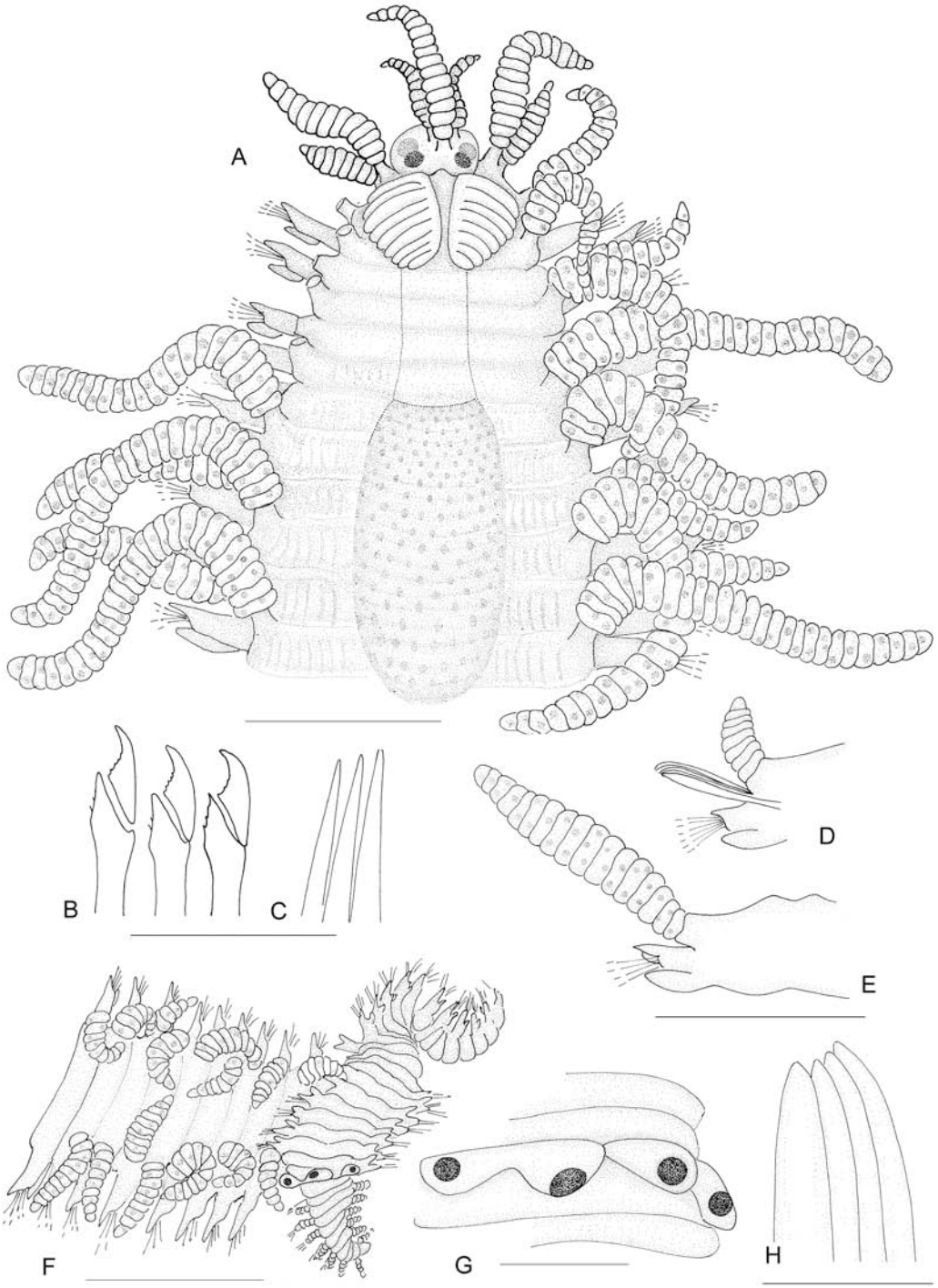

Figure 8. *Nuchalosyllis lamellicornis*. (A) Anterior end, dorsal view; (B) Midbody falcigers; (C) Midbody aciculae; (D) parapodium of stolon, anterior view; (E) Midbody parapodium, anterior view; (F) Posterior end in regeneration and stolon, dorsal view; (G) Prostomium of developing stolon; (H) Natatory chaetae. Scale bars A, 1 mm; B, C, H, 48 ! m; D, E, 1.8 mm; F, 1.2 mm; G, 0.2 mm.

regenerating posterior end (Fig. 8F). Stolon with yellowish to orange body, dorsal cirri partially pigmented in orange. Stolon's head in development, visible in ventral position. Two pairs of eyes on lateral sides of prostomium on two cephalic lobes, dark reddish; posterior pair larger than anterior one (Figs 8F, G). Palps reduced or absent. Dorsal cirri with 5-6 articles, cirrophores well developed. Ventral cirri slightly longer than parapodia lobes, digitiform to lanceolate (Fig. 8D). Conical neuropodia with pre and postchaetal lobes with about 5 unidentate falcigers (Fig. 8D). Wide and long notochaetae, laceolate in shape, in many cases fused along their length forming paleae (Figs 8D, H).

Distribution

Brazil.

Genus *Odontosyllis* Claparède, 1863

Odontosyllis Claparède, 1863: 47. San Martín & Hutchings, 2006: 281-282.

Alluaudella Gravier, 1905: 372.

Type species

S*yllis fulgurans* Audouin & Milne Edwards, 1833.

Diagnosis

(Modified from San Martín & Hutchings, 2006). Body of variable size, 5-10 mm in length, with numerous cylindrical segments. Prostomium with 4 eyes, and sometimes a pair of anterior eyespots. Three antennae. Palps broad, free for almost all their length, fused basally. Peristomium usually reduced dorsally; 2 pairs of tentacular cirri. Occipital flap present, usually well developed, covering peristomium dorsally and prostomium partially. Nuchal organs as 2 ciliated grooves between prostomium and peristomium, sometimes extending to lateral areas of prostomium. Dorsal cirri elongated, smooth, distally tapered, but sometimes short or indistinctly articulated. Parapodia usually with pre- and postchaetal lobes. Ventral cirri digitiform to pillow-shaped. Compound chaetae heterogomph, usually with shafts distally spinose. Dorsal and ventral simple chaetae

present on some parapodia. Pharynx short, distinctly shorter than proventricle, provided with a few teeth, directed backwards, pharyngeal mid-dorsal tooth absent; pharynx when not everted situated posteriorly to chaetiger 1. Proventricle usually long and wide and massive. Pygidium with 2 anal cirri. Reproduction by epigamy; epigamic specimens sometimes strongly modified and phosphorescent.

Remarks

San Martín & Hutchings (2006) suggested that *Alluaudella* could be a synonymous with *Odontosyllis*, however they could not revise the type series. In that paper, they provide a complete list of synonymies. The genera *Fauvelia* Gravier, 1900; *Atelesyllis* Pruvot, 1930; *Eurymedusa* Kinberg, 1865 and *Synpalposyllis* Hartmann-Schröder, 1983 may well be synonymous with *Odontosyllis* too, their type series however have been lost or they consist only in one juvenile without clear diagnostic features (*Synpalposyllis*).

Odontosyllis madagascariensis (Gravier, 1905) n. comb.

(Figure 9)

Alluaudella madagascariensis Gravier, 1905: 372-376, figs. 1-5. Day, 1967: 279, 278.

Material examined

Holotype MNHN 279 and 2 paratypes MNHN280, Madagascar, Fort Dauphin, coll. by Allan, 1/01/1901.

Additional material examined

Alluaudella longocirrata Murad & Mohamad, 1973. Holotype NHML 1971.43, Kuwait, Al-Najafa, 29º 16'N 48º05'E, intertidal in rock cleft, 1/08/1969.

Description

Body broad anteriorly, tapered posteriorly. Holotype is fragmented in two parts, 8 mm long in total with 51 segments, anterior end 3 mm long, 1 mm wide. Two paratypes, with several fragments, 5 mm and 3 mm long, both 0.9 mm wide. Colour pattern consisting on

transversal black or dark brownish bands on posterior end of each segment and black spots irregularly distributed over dorsum of anterior segments. Some paratypes without colour pattern. Dorsum of body markedly arched. Prostomium oval, large; 4 eyes in open trapezoidal arrangement; median antenna short, conical, shorter than prostomium, originating between posterior eyes (Fig. 9A). Lateral antennae short and conical, similar in length to median one, originating near anterior margin of prostomium, close to median antenna (Fig. 9A). Palps reduced, shorter than prostomium, ventrally folded. Nuchal organs as two ciliated pits between prostomium and peristomium. Peristomium dorsally reduced. Large occipital flap covering posterior part of prostomium. Tentacular cirri digitiform, both similar in size, longer than antennae (Fig. 9A). Dorsal cirri more elongated than antennae and tentacular cirri, shorter than half of body width, as long as parapodial lobe on anterior segments, half longer than parapodial lobe on posterior segments (Figs 9A, E). Dorsal cirri alternating in their insertion and orientation, those arising from dorsal position directed dorsally; those arising from ventral position directed ventrally (Fig. 9E). Parapodial lobes elongated, lateroventrally directed, almost rectangular, with one prechaetal lobe and two postchaetal lobes, anterior one slightly longer than posterior ones (Fig. 9C). Progressively, posterior parapodia becoming more elongated, parapodial lobes more distinct. Ventral cirri digitiform, not reaching or extending beyond parapodial lobes (Fig. 9C); 12 simple chaetae per parapodia, apparently shafts of compound chaetae (Fig. 9D). Ventral simple chaetae on posterior parapodia, thin, smooth. Dorsal simple chaetae not observed. Parapodia with one pointed acicula (Fig. 9F). Pharynx short and wide, through 2-3 segments (Fig. 9A), with 2 lateral plates (Fig. 9B). Proventricle wide, short, barrel-shaped slightly longer than pharynx, through about 5 segments (Fig. 9A), with 35 muscle cell rows in paratype, not visible in the holotype. Pygidium missing on the examined specimens.

Remarks

Gravier (1905) and later Day (1967) considered that this species lacked ventral cirri and principally because of this characteristic, they placed it in a new genus. After detailed examination, we saw ventral cirri on each parapodium, inserted on the proximal half of parapodia and in many cases joined to the parapodia, though possibly fused during the

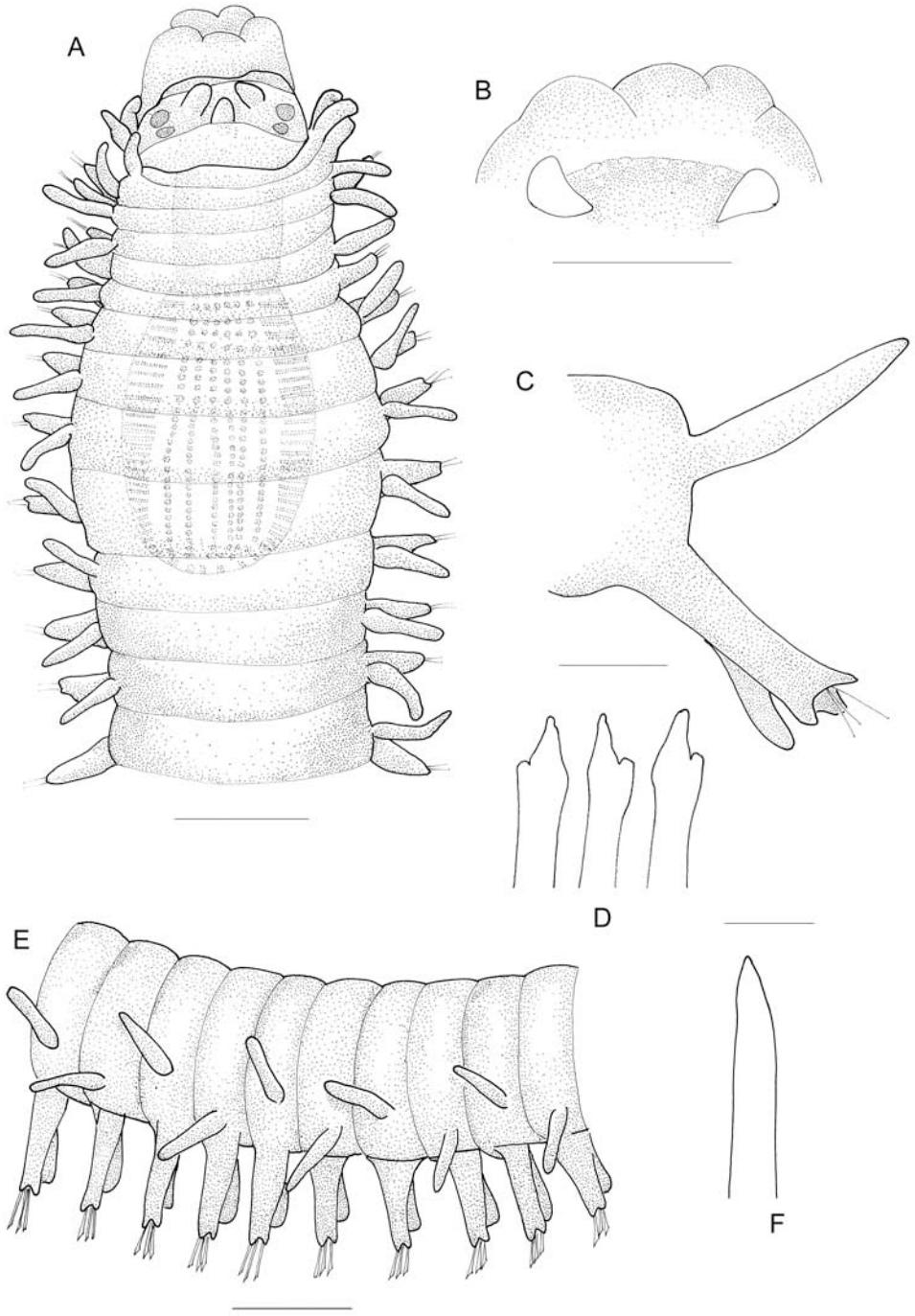

Figure 9. *Odontosyllis madagascarensis* n. comb. (A) Anterior end, dorsal view; (B) lateral plates on pharynx; (C) Midbody parapodium, anterior view; (D) Midbody chaetae; (E) Midbody segments, lateral view; (F) Midbody acicula. Scale bars A, E, 0.5 mm; B, 0.25 mm; C, 0.15 mm; D, F, 12.5 ! m.

preservation porcess. Gravier (1905) dissected one paratype and described the terminal part of the pharynx with papillae but he did not observe any kind of armature. After examining the dissected paratype we agree in that it is difficult to observe any teeth, but two lateral plates, common in the trepan of *Odontosyllis*, were evident. Another characteristic mentioned in the previous descriptions was the presence of spherical tentacular cirri. However, the tentacular cirri are bent in the holotype. In a dorsal view they seem to be oval but in a lateral position it is possible to appreciate its distal part. They are slightly shorter than the dorsal cirri but the difference in length is not significant. Finally the chaetae were described as simple chaetae, although Day (1967) considered them as shafts without blades, which were probably lost. We agree with the latter hypothesis since they are quite similar in shape to common shafts of Syllidae. None of the specimens present blades but the type series consists only in the holotype and two paratypes plus several fragments, therefore it is quite possible that all of them have lost their blades.

The studied species shares several diagnostic characteristics with *Odontosyllis*: Presence of an occipital flap, shape and length of dorsal and ventral cirri, elongated parapodia with several long pre- and postchaetal lobes, lateral plates in the pharynx and probably teeth, short and spherical proventricle and short and considerably wide pharynx. Although the presence of the typical trepan of *Odontosyllis* was not clearly observed, we consider that there are enough similarities to assign this species to genus *Odontosyllis*. The only other species of the genus, *A. longocirrata*, was synonymized with *O. freycinetensis* by San Martín & Hutchings (2006). The holotype of this species also lacked a complete trepan but San Martín & Hutchings (2006) argued that the specimen was a juvenile and this characteristic might not be present in juvenile individuals. This too, might be the explanation for the absence of teeth *in O. madagascarensis* since the specimens were all small (3-8 mm) (adult specimens in *Odontosyllis* are generally 20-40 mm long). *Odontosyllis freycinetensis* is also similar to *O. madagascariensis* in the colour pattern and long parapodia, however its dorsal cirri are not inserted at different levels, as they are in *O. madagascariensis*. Other similar species of *Odontosyllis* are *O. annulatus* (Hartmann-Schröder, 1979) and *O. globulocirrata* Hartmann-Schröder, 1981, both from Australia. *Odontosyllis annulatus* was originally described without ventral cirri

as Gravier (1905) described *O. madagascariensis*; however, it has ventral cirri distally inserted and practically fused to parapodia (San Martín & Hutchings, 2006). Both species are different principally because ventral cirri and parapodia in *O. annulatus* are considerably shorter. *Odontosyllis globulocirrata* is similar to *O. madagascariensis* in the presence of dorsal cirri inserted alternatively at different levels on each segment. Besides, the specimen dissected by San Martín & Hutchings (2006) did not have a trepan. Nevertheless, they are remarkably different in the shape and size of dorsal cirri, which are spherical in *O. globulocirrata*.

Distribution

Madagascar.

Genus *Parexogone* (Mesnil & Caullery, 1918)

Parexogone Mesnil & Caullery, 1918: 125. San Martín, 2005: 108.

Exogonella Hartman, 1961: 74.

Type species

Paedophylax hebes Webster & Benedict, 1884.

Diagnosis

Modified from San Martín (2005). Body small, meiofaunal, surface smooth. Prostomium with 3 antennae; usually 4 eyes, sometimes also with 2 eye spots. Palps well developed, completely fused to each other or with terminal notch. Single pair of minute tentacular cirri. Dorsal cirri usually small, papilliform to oval, present on all segments or absent on chaetiger 2 in adults of some species. Compound chaetae with heterogomph articulations, falcigers all similar in shape and blade length, sometimes psudospinigers with simple shaft tips, blades relatively similar to falcigers but longer. Dorsal simple chaetae similar throughout body, tips unidentate or bidentate, with both teeth similar. Ventral simple chaetae on posterior parapodia. Two usually long anal cirri present. Pharynx with anterior margin surrounded by soft lobes, with anterior tooth. Mature

females carrying eggs ventrally, developing to embryos and juveniles, lacking capillary notochaetae (natatory chaetae); mature males with long natatory chaetae; some species viviparous.

Remarks

Parexogone was initially considered to be a subgenus of *Exogone* Örsted, 1845 by San Martín (1991). It was later promoted to generic category by Böggemann &Westheide (2004).

Parexogone brunnea (Hartman, 1961)

(Figure 10)

Exogonella brunnea Hartman, 1961: 74-75, pl. 8, figs. 1-5; 1965: 430, 431.

Material examined

Holotype NHMLAC 14,811, Point Vicente, San Pedro area, Southern California, shelf and slope depths, in sediments of black mixed silt and sand.

Description

Body small, cylindrical, holotype complete 4 mm long, and 0.3 mm wide, with 48 segments. Prostomium ovate to rectangular, wider than long; eyes not observed (four small eyes spots in the posterior half of prostomium, *fide* Hartman, 1961); antennae short, papilliform, all similar in size. Median antenna inserted on posterior part of prostomium and partially covered by peristomium, slightly posteriorly located. Palps broad, longer than prostomium, fused along their length, anterior end bluntly conical (Fig. 10A). Peristomium shorter than subsequent segments, covering dorsally posterior part of prostomium; tentacular cirri papilliform, similar to lateral antennae. Dorsal cirri on all segments, papilliform similar in size and shape to tentacular cirri and antennae. (Fig. 10A). Ventral cirri papilliform, not reaching tips of parapodial lobes. Anterior chaetigers with 6 compound chaetae, 2 pseudospinigers with elongate blades (32 ! m), unidentate, distal tooth larger than proximal one; blades with long, erect, fine spines on cutting edge

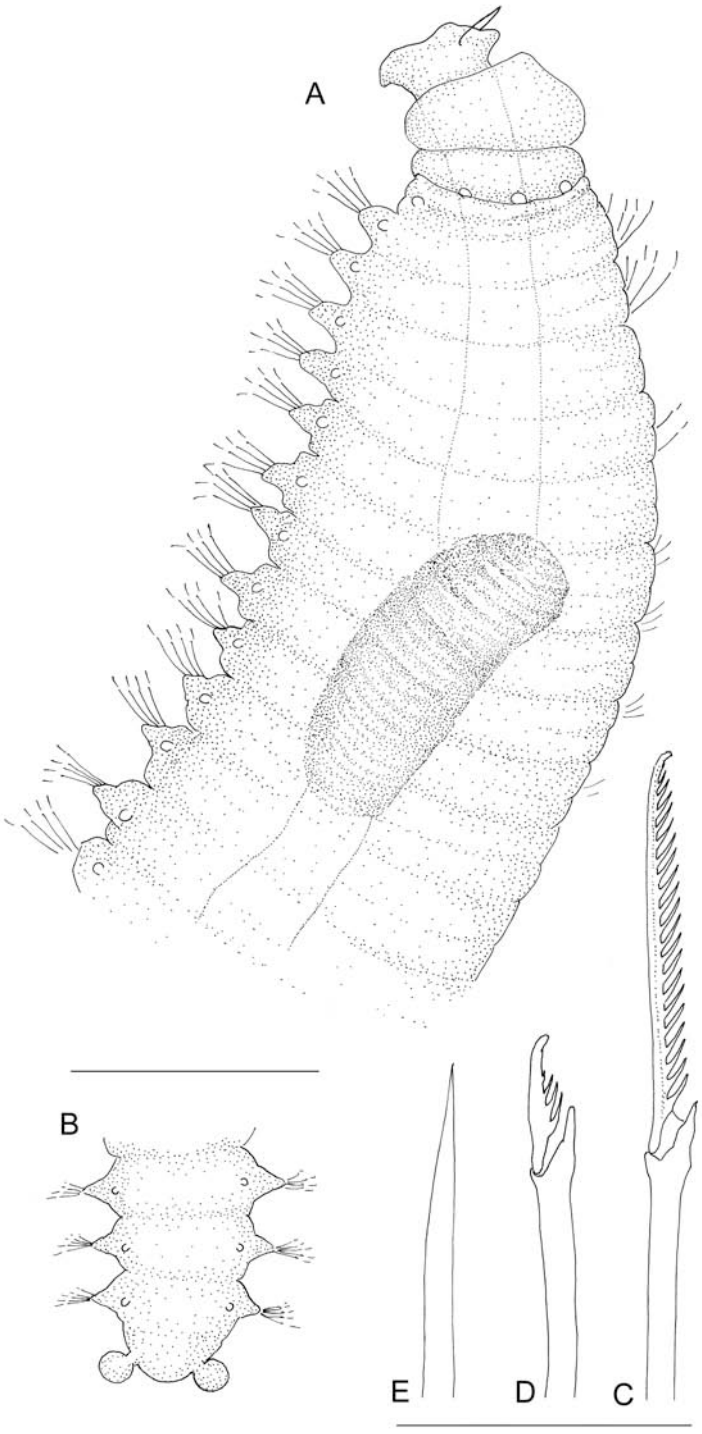

Figure 10. *Parexogone brunnea* n. comb. (A) Anterior end, dorsal view; (B) posterior end, dorsal view; (C) Superior chaeta, anterior parapodium; (D) Inferior chaeta, anterior parapodium; (E) Simple dorsal chaeta, midbody parapodium. Scale bars A, 0.2 mm; B, 0.25 mm; C-E, 24 ! m.

(Fig. 10C); 4 falcigers with short blades (6 ! m), unidentate, with fine spines on proximal side of cutting edge (Fig. 10D). Posterior parapodia with 4 compound chaetae; one pseudospiniger, shorter than anterior ones (19 ! m); 4 falcigers (6 ! m). Dorsal simple chaeta on posterior-most parapodium, straight, unidentate (Fig. 10E). Ventral simple chaetae not observed. Pygidium conical, with two spherical anal cirri, larger than dorsal cirri and antennae (Fig. 10B). Pharynx through 6 segments; pharyngeal tooth conical, on anterior edge (Fig. 10A). Proventricle short, through 4-5 segments (Fig. 10A), muscle cell rows not clearly visible.

Remarks

The monotypic genus *Exogonella* was described as a new taxon, as the species *E. brunnea* was reported to lack antennae and dorsal cirri. However, after a detailed study, we found that the holotype has three minute, papilliform antennae on the posterior part of the prostomium, and tentacular and dorsal cirri similar to antennae on each parapodium. This species has similar characteristics to the *Parexogone* species and it is herein transferred to that genus. The eyes were not distinguished in this revision, probably due to the poor state of preservation.

Distribution

Southern California.

Nomina dubia taxa

Exogonoides antennata Day, 1963

(Figure 11)

Exogonoides antennata Day, 1963: 403-404, text-fig. 5 j-n. Day, 1967: 279, fig. 12.11 s-w.

Material examined

Holotype NHML 1963.1.34, S. coast of Cape Provence, 34º 02'S 23º 28,4'E, 49 m, sand and rocks, 29/11/60, coll. by Prof J.H. Day. Paratype NHML 1963.1.35, S. coast of

Cape Provence, 34º 02'S 23º 28.4'E, 49 m, sand and rocks, 29/11/60, coll. by Prof J.H. Day.

Description

Holotype anterior fragment with more than 200 segments, 35 mm long and 0.5 mm wide. Paratype posterior fragment. Body cylindrical, broad and slender, cream coloured with black vertical marks on dorso-lateral sides of posterior segments and pygidium (Fig. 11F). Prostomium wider than long, elliptical. Two pairs of eyes, crescent-shaped; located on anterior half of prostomium; anterior pair larger than posterior one (Fig. 11A). Ocular spots absent. Five anterior lobes, ovoids; three of them more dorsally located (antennae, *fide* Day, 1963) inserted on anterior part of prostomium, all similar in length. Remaining two lobes ventrally located (palps, *fide* Day 1963), shorter than dorsal ones, not visible dorsally, and not fused (Fig. 11 A, B). Peristomium similar in length to following segments. One pair of tentacular cirri, ovoid. Dorsal cirri spherical to ovoid, increasing in size towards posterior part. Ventral cirri fused to ventral margin of parapodia (Fig. 11C). Holotype with three compound heterogomph chaetae per parapodium, with short blades (6-8 ! m), bidentate, both teeth similar in size and fine spines on cutting edge of blades (Fig. 11D). Paratype with three simple chaetae per parapodium, morphologically similar to shafts of chaetae of holotype, but they are larger and distally expanded, triangular with serration on cutting edge of blades (Fig. 11E). Aciculae not seen. Pygidium conical with one anal cirri, ovoid, similar to dorsal cirri (Fig. 11F). Pharynx and proventricle not present (holotype dissected) (pharynx through 6 segments and proventricle with 15 muscle row cells, trepan and pharyngeal tooth absent, *fide* Day, 1963).

Remarks

Day (1963) considered this species similar to *Exogone* in the antennae, tentacular and dorsal cirri shape, although a possible similarity with Autolytinae was also suggested. In the original description, the holotype was considered to be an anterior fragment and the paratype a posterior fragment. We agree with this interpretation, and we add that both fragments could actually belong to the same animal, because the segment at which the holotype is fragmented coincides with the first segment of the paratype. Simple chaetae

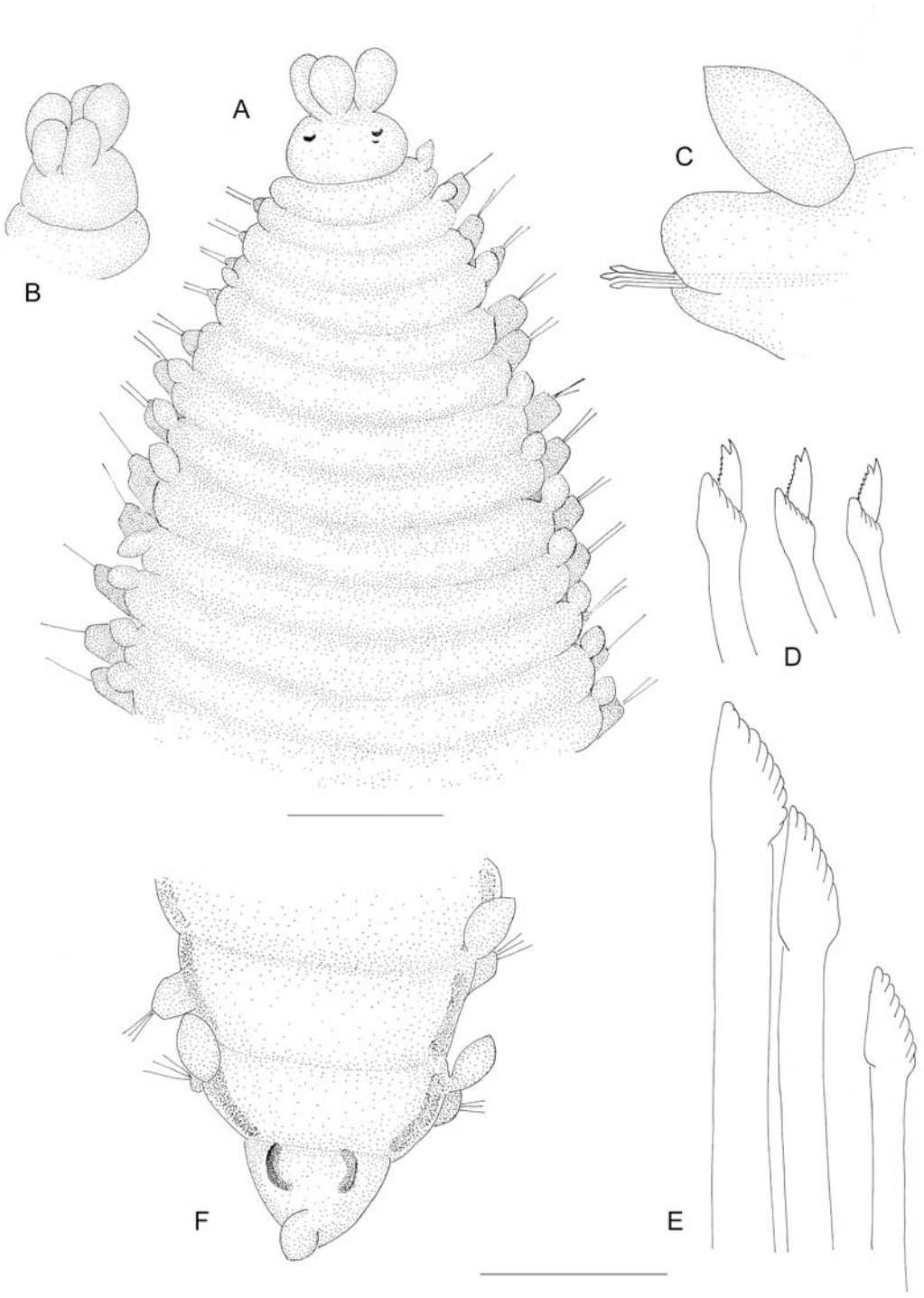

Figure 11. *Exogonoides antennata* incertae-sedis. (A) Anterior end, dorsal view, holotype; (B) Anterior end, ventral view, holotype; (C) Midbody parapodium, anterior view, paratype; (D) Anterior chaetae, holotype; (E) posterior chaetae, paratype; (F) Posterior end, dorsal view, paratype. Scale bars A, B, F, 0.2 mm; C, 92 ! m; D, E, 20 ! m.

in posterior chaetigers seem to be the result of an enlargement of shafts and loss of blades. Although simple chaetae of several Syllidae species are supposed to have the same origin (e. g. *Syllis amica* Quatrefages, 1865, *Syllis ferrani* Alós & San Martín, 1987, *Opisthosllis japonica* Imajima, 1966, *Haplosyllis onthogorgicola* Martín, Núñez, Riera & Gil, 2002, etc), chaetae of *Exogonoides* are different to those of any described species. Moreover, pharynx and proventricle could not be examined since they were not preserved after dissection, consequently possible similarities and differences with the common proventricle of Syllidae could not be assessed. As some characteristics are different to any other species of the family and as we could not check the presence of a proventricle, we believe this taxon should be considered *nomina dubia*.

Distribution

Agulhas Bank, South Africa.

DISCUSSION

The genera *Alluaudella*, *Braniella* and *Exogonella* are considered to be non valid, they have been synonymized with *Odontosyllis*, *Anguillosyllis* and *Parexogone*, respectively. Otherwise, *Brachysyllis* is considered herein as a valid genus, exhibiting clear differences from *Dioplosyllis*. The relationships between *Anguillosyllis*, *Clavisyllis*, *Brachysyllis*, *Lamellisyllis* and *Nuchalosyllis* and the rest of Syllidae still prove difficult to stablish, despite their revision. These, in fact, show a combination of traits which does not fit the diagnosis of any of the traditionally recognized subfamilies.

Other recently described genera are also difficult to assign to any subfamily. For instance, *Nooralia* San Martín, 2002 possesses a peculiar system of brooding carrying eggs attached to dorsal chaetae. This genera was provisionally placed within Exogoninae, despite not fully coinciding with the diagnosis (San Martín, 2002). *Karroonsyllis* San Martín & López, 2003 is a genus with a mixture of traits typical of the Exogoninae and Syllidae subfamilies, and was provisionally placed within Syllinae due to the presence of articulated cirri (San Martín & López, 2003). *Paraopisthosyllis* Hartmann-Schröder, 1991

was provisionally assigned to Eusyllinae despite the fact that its dorsal cirri could be considered as articulated (with only one article), and its reproductive mode is still unknown (San Martín & Hutchings, 2006). Finally, *Murrindisyllis* San Martín, Aguado & Murray, 2007, is a recently described genus showing a combination of traits between Exogoninae and Eusyllinae (San Martín *et al*., 2007). All these examples show that there are too many exceptions to the rule.

There are few phylogenetic studies on Syllidae and they are principally focussed in particular processes, such as reproductive modes (Nygren, 1999; Nygren & Sundberg, 2003) or in specific groups, e.g. Autolytinae (Nygren, 2004) or *Typosyllis* (Licher, 1999). These studies revealed that some of the traditional subfamilies, as Eusyllinae, might be paraphyletic. However, these studies are still insufficient to reach a robust understanding of Syllidae as a whole. The combination of different techniques, methodologies and sources of data is becoming increasingly necessary in aiming to comprehend the biology of this group. Revisions of historical material, such as the one presented herein, shall also help shed new light in our understanding of the evolutionary paths taken by these fascinating animals.

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BLOQUE III

ESTUDIO FILOGENÉTICO DE LA FAMILIA SYLLIDAE

Photo by A. Nygren

1. Phylogeny of Syllidae (Polychaeta) based on combined molecular analysis of nuclear and mitochondrial genes. Aguado, M.T.; Nygren, A. & Siddall, M. E. 2007. *Cladistics.*

2. Phylogeny of Syllidae (Phyllodocida, Annelida) based on morphological data.

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Phylogeny of Syllidae (Polychaeta) based on combined molecular analysis of nuclear and mitochondrial genes

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Abstract

The phylogeny of Syllidae is assessed in a combined analysis of molecular data from nuclear 18S rDNA and mitochondrial 16S rDNA and cytochrome *c* oxidase subunit I. In total, 103 terminal taxa are examined: 88 syllids in the four classical subfamilies Eusyllinae, Exogoninae, Syllinae and Autolytinae, as well as 15 outgroup taxa from Phyllodocida and Eunicida. Maximum parsimony analysis of the combined data set indicates that Syllidae, as currently delineated, is monophyletic, though not with very high support values. *Astreptosyllis* Kudenov & Dorsey, 1982, *Streptosyllis* Webster & Benedict, 1884 and *Syllides* Örsted, 1845 comprise a monophyletic group well differentiated from the rest of the Syllidae. The subfamilies Autolytinae and Syllinae are monophyletic. Exogoninae is monophyletic, although not well supported, and Eusyllinae is clearly paraphyletic. Results corroborate previous studies about the evolution of reproductive modes in that epigamy is the plesiomorphic condition and schizogamy appeared independently in Autolytinae and Syllinae.

Syllidae is one of the largest families of polychaetes, comprising more than 700 described species in more than 70 described genera (Pleijel, 2001a; San Martín, 2003). Syllids are highly diversified and occur in all marine benthic habitats. They are easily recognized by the presence of a muscularized region of the anterior digestive tract, the proventricle that probably works as a suctorial-feeding structure (Fauchald and Jumars, 1979; Glasby, 2000). Syllid taxonomy is not well established and though new species and genera are being described, the relationships among them remain poorly characterized (Pleijel, 2001a). The current classification into four subfamilies (Syllinae Grube, 1850; Exogoninae Langerhans, 1879; Eusyllinae Malaquin, 1893; and Autolytinae Langerhans, 1879) is considered unsatisfactory because it does not rely on phylogenetic systematics and it appears to be in use only for practical reasons (Fauchald, 1977; Glasby, 2000; San Martín and López, 2003; San Martín, 2003). The presence of a proventricle has been considered the synapomorphy of the group (Glasby, 1993), although other groups such as Sphaerodoridae may share this feature (Fauchald and Rouse, 1997; Rouse and Fauchald, 1997; Pleijel, 2001b).

Syllids present some of the most spectacular sexual reproductive processes in invertebrates (Franke, 1999; Nygren, 1999; San Martín, 2003). There are two principal reproductive modes: epigamy (the whole animal is involved) and schizogamy (by stolons deriving from the posterior part). Moreover, there are two types of schizogamy: gemmiparity (developing series of several stolons) and scissiparity (only one stolon). Epigamy is reported in several genera of Eusyllinae and Exogoninae and in *Epigamia* (Nygren, 2004) (Autolytinae). It is also present in other groups of polychaetes, such as Nereididae, Phyllodocidae, Glyceridae, Scalibregmatidae, Nephtyidae, Spionidae, Amphinomidae, Eunicidae and Opheliidae (Rouse and Pleijel, 2001). Scissiparity

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occurs in Syllinae and Autolytinae, whereas gemmiparity occurs principally in Autolytinae [a different manifestation of gemmiparity may exist in *Trypanosyllis gemmipara* Johnson, 1901 and *Trypanosyllis asterobia* (Okada, 1933)]. Scissiparity also is known for some groups of Eunicida, while gemmiparity is unique to syllids (Pleijel and Rouse, 2006). Viviparity is reported in several species of *Syllis* Lamark, 1818, *Dentatisyllis* Perkins 1981 and *Exogone* Örsted, 1845 (Franke, 1999; San Martín, 2003; Pleijel and Rouse, 2006).

Two different egg brooding modes have been reported in Exogoninae. Species in the genera *Prosphaerosyllis* San Martín, 1984, *Salvatoria* McIntosh, 1885, *Erinaceusyllis* San Martín, 2005 and *Cicese* Díaz Castañeda & San Martín, 2001 carry eggs attached to notochaetae. Those in the genera *Exogone*, *Parapionosyllis* Fauvel, 1923, *Sphaerosyllis* Claparède, 1863 and *Brania* Quatrefages, 1866 carry eggs attached to the nephridial pore and postembryonic development is direct, without larval stages (San Martín, 2005). A special case is found in *Nooralia* San Martín, 2002, an enigmatic genus from Australia that carries eggs attached to compound neurochaetae (San Martín, 2002). Several authors have suggested that these brooding modes correspond to different evolutionary lines in Exogoninae (Mastrodonato et al., 2003; San Martín, 2003, 2005). Brooding of eggs has been also reported in some genera traditionally included in Eusyllinae. Ventral brooding is exhibited by some species of *Syllides* Örsted, 1845, such as *Syllides benedicti* Banse, 1971 and *Syllides japonicus* Imajima, 1966 (Heacox and Schröeder, 1978; Nygren, 1999; San Martín, 2003), and by each of *Pionosyllis augeneri* (Hartmann-Schröder, 1979) and *Pionosyllis longisetosa* (Hartmann-Schröder, 1990). Dorsal brooding is characteristic of *Nudisyllis pulligera* (Krohn, 1852) (Pierantoni, 1905; Augener, 1913; Hartmann-Schröder, 1979; San Martín, 2005). Members of Autolytinae exhibit a different kind of parental care in which the female stolon cares for the young in one or several ventral egg sacs (Gidholm, 1965; Nygren, 1999).

There are four prior cladistic studies of the Syllidae (Licher, 1999; Nygren, 1999; Nygren and Sundberg, 2003; Nygren, 2004). Licher (1999) focused on a revision of all species included in the genera *Syllis* and *Typosyllis* Langerhans, 1879 using morphological characters (herein, the latter genus is considered a junior synonym of *Syllis*). He also suggested, though not on a phylogenetic basis, that *Syllides*, *Astreptosyllis* Kudenov & Dorsey, 1982, *Streptosyllis* Webster & Benedict, 1884 and *Streptospinigera* Kudenov, 1983 together comprise the sister group of the rest of syllids (Licher, 1999). Licher (1999) also proposed that Eusyllinae was paraphyletic and that Exogoninae, Autolytinae and Syllinae each were monophyletic. Nygren (1999) examined the evolution of reproductive modes in Syllidae based on morphological characters from 12 representatives of the group. Nygren and Sundberg (2003) reconsidered the evolution of reproductive modes in Autolytinae based on 16S rDNA and 18S rDNA sequences for 31 representatives of the group. Nygren (2004) later completely revised the subfamily Autolytinae with combined morphological and molecular data. The three studies coincided in corroborating Autolytinae, Syllinae and Exogoninae each as monophyletic, whereas Eusyllinae was paraphyletic. Epigamy was found to be the plesiomorphic reproductive mode in Syllidae with schizogamy appearing in Syllinae and Autolytinae as separate events. The more detailed aspects of evolution of reproductive modes within Autolytinae remained ambiguous.

Syllidae was placed within Phyllodocida by Rouse and Fauchald (1997; see Rouse and Pleijel, 2001), a clade containing a large number of families, and specifically in Nereidiformia (Pleijel and Dahlgren, 1998; Rouse and Pleijel, 2001). The latter postulates monophyly of Syllidae together with Chrysopetalidae, Hesionidae, Nautiliniellidae, Nereididae and Pilargidae. Molecular data have proven to be an important tool for resolving relationships among polychaetes (e.g., Brown et al., 1999; Bleidorn et al., 2003a,b; Rousset et al., 2007). Between them, rDNA sequences have been widely used to estimate relationships within specific groups of annelids (e.g., Apakupakul et al., 1999; Martin et al., 2000; Rousset et al., 2003; Hall et al., 2004), and also for estimating relationships among closely related taxa (Nygren and Sundberg, 2003; Bleidorn, 2005; Siddall et al., 2005). Our study aims to resolve the phylogenetic relationships among genera and subfamilies in Syllidae while testing monophyly of the group by using three different genes. Further, it aims to continue investigations into the evolution of reproductive modes and some morphological features.

Materials and methods

Taxon sampling

The terminal taxa were selected in order to examine the four classical subfamilies. The genera included herein and the current taxonomic situation for Syllidae are shown in Table 1. Relative representation of genera in comparison with the total number in each subfamily are: 10 genera of Eusyllinae (32%); seven genera of Syllinae (33%); four genera of Autolytinae (46%) and seven of Exogoninae (70%). Included species are listed in Table 2 with GenBank accession numbers and sampling areas/sites. Several syllid terminals from GenBank are redundant with others collected for this study; both were included in the analysis to examine possible contamination, incorrect identifications or differences between morphologically indistinguishable specimens. Collected worms were fixed and preserved in

Table 1
Current classification of outgroup species and syllid genera selected for this study (Rouse and Pleijel, 2001; San Martín, 2003; Nygren, 2004)

POLYCHAETES
Palpata
Aciculata, Eunicida
Eunicidae Berthold, 1827
Eunice pennata (Müller, 1776)
Aciculata, Phyllodocida
Sphaerodoridae Malmgren, 1867
Sphaerodoropsis philippi (Fauvel, 1911)
Sphaerodoropsis anae Aguado and Rouse, 2006
Phyllodocidae Örsted, 1843
Phyllodoce maculata (Linnaeus, 1767)
Aphroditiformia
Aphroditoidea Malmgren, 1867
Polynoidae
Lepidonotus squamatus (Linnaeus, 1758)
Harmothoe imbricata (Linnaeus, 1767)
Paralepidonotus ampuliferus (Grube, 1878)
Sigalionidae Kinberg, 1856
Sigalion bandaensis Horst, 1917
Sthenelais boa (Johnston, 1833)
Pisionidae Ehlers, 1901
Pisione remota (Southern, 1914)
Nereidiformia
Nereididae Johnston, 1865
Ceratonereis longiceratophora Hartmann-Schröder, 1985
Nereis pelagica Linnaeus, 1758
Chrysopetalidae Ehlers, 1864
Chrysopetalidae sp.
Pilargidae Saint-Joseph, 1899
Sigambra sp.
Hesionidae Grube, 1850
Hesiospina sp.
Syllidae Grube 1850
Subfamily Syllinae Grube, 1850
Branchiosyllis Ehlers, 1887
Eurysyllis Ehlers, 1864
Geminosyllis Imajima, 1966
Haplosyllis Langerhans, 1879
Opisthosyllis Langerhans, 1879
Syllis Lamark, 1818
Trypanosyllis Claparède, 1864
Subfamily Exogoninae Langerhans, 1879
Brania Quatrefages, 1866
Erinaceusyllis San Martín, 2005
Exogone Örsted, 1845
Parapionosyllis Fauvel, 1923
Prosphaerosyllis San Martín, 1984
Salvatoria McIntosh, 1885
Sphaerosyllis Claparède, 1863
Subfamily Eusyllinae Malaquin, 1893
Amblyosyllis Grube, 1857
Astreptosyllis Kudenov and Dorsey, 1982
Dioplosyllis Gidholm, 1962
Eusyllis Malmgren, 1867
Nudisyllis Knox and Cameron, 1970
Odontosyllis Claparède, 1863
Opisthodonta Langerhans, 1879
Pionosyllis Malmgren, 1867
Streptosyllis Webster and Benedict, 1884
Syllides Örsted, 1845
Subfamily Autolytinae Langerhans, 1879
Epigamia Nygren, 2005
Myrianida Milne Edwards, 1845
Proceraea Ehlers, 1864
Procerastea Langerhans, 1884
Virchowia Langerhans, 1879

Table 2
Taxa used for phylogenetic analysis of Syllidae. GB: from GenBank; (a) Nygren and Sundberg (2003); (b) Hall et al. (2004); (c) Colgan et al. (2006) (d) Worsaae et al. (2005); (e) Dahlgren et al. (2001); (f) Siddall et al. (2001); (g) Rousset et al. (2007); (h) Rousset et al. (2004); (i) Maxmen et al. (2003); (j) Wiklund et al. (2005); (k) Dahlgren et al. (2000)

Taxon	Locality	GenBank accession no.		
		18S	CO-I	16S
Ingroup				
Amblyosyllis formosa (Claparède, 1863)	Banyuls, France	EF123834	EF123745	–
Amblyosyllis sp. GB	Banyuls, France	AF474284 a		
Astreptosyllis acrassiseta Kudenov and Dorsey, 1982	Sydney, Australia	–	–	EF123787
Branchiosyllis exilis (Gravier, 1900)	Port de la Selva, Girona, Spain	–	EF123746	–
Branchiosyllis sp. GB	La Jolla, California, USA	AF474283 a	–	–
Brania arminii (Langerhans, 1881)	Cádiz, Spain	EF123831	–	–
Brania pusilla (Dujardin, 1851)	Vigo, Spain	EF123838	–	–
Dioplosyllis sp.	Banyuls, France	EF123827-8	–	–
Epigamia magna (Berkeley, 1923) GB	Washington, USA	AF474309 a	–	AF474263 a
Epigamia noroi (Imajima and Hartman, 1964)	California, USA	–	EF123747	EF123820
Epigamia noroi GB	California, USA	AF474310 a	–	AF474264 a
Erinaceusyllis belicensis (Russell, 1989)	Cádiz, Spain	EF123823-4	–	–
Erinaceusyllis hartmannschroederae San Martín, 2005	Sydney, Australia	EF123868	–	–
Eurysyllis tuberculata Ehlers, 1864	Banyuls, France	EF123833	EF123748	–
Eusyllis blomstrandi Malmgren, 1867	Kaldbak, Faroe Islands	EF123887	EF123749	EF123788
Eusyllis blomstrandi GB	Kaldbak, Faroe Islands	AF474281 a	AY839579 j	–
Exogone naidina Örsted, 1845	Wales, UK	EF123886	–	–
Exogone naidina GB	Wales, UK	AF474290 a	–	–
Geminosyllis ohma Imajima, 1966	St. Juan, Washington, USA	EF123883	EF123750	EF123789
Haplosyllis sp.	Sydney, Australia	–	–	EF123790
Haplosyllis spongicola Grube, 1855	Banyuls, France	EF123837	EF123751	EF123791
Haplosyllis spongicola GB	Banyuls, France	AF474291 a	–	–
Myrianida convoluta (Cognetti, 1953) GB	California, USA	AF474303 a	–	AF474257 a
Myrianida pachycera (Augener, 1913) GB	California, USA	AF474304 a	–	AF474258 a
Myrianida sp.	Galicia, Spain	EF123855	EF123752	–
Myrianida pinnigera (Montagu, 1808)	Cádiz, Spain	EF123843	EF123753	–
Myrianida pinnigera GB	Cádiz, Spain	AF474298 a	–	AF474252 a
Myrianida prolifera (O.F. Müller, 1788) GB	Kristineberg, Sweden	AF474295 a	–	AF474249 a
Nudisyllis pulligera (Krohn, 1852)	Port de la Selva, Girona, Spain	EF123873	EF123754	–
Nudisyllis pulligera GB	Banyuls, France	AF474286 a	–	–
Odontosyllis fulgurans (Audouin and Milne Edwards, 1834)	Port de la Selva, Girona, Spain	EF123882	EF123755	EF123792
Odontosyllis gibba Claparède, 1863	Port de la Selva, Girona, Spain	EF123850	EF123756	EF123793
Odontosyllis gibba GB	Anglesey, Wales	AF474282 a	–	–
Opisthodonta morena Langerhans, 1879 GB	Banyuls, France	AF474285 a		
Opisthosyllis leslieharrisae Aguado, San Martín and Nygren, 2005	California, USA	EF123844	EF123757	–
Parapionosyllis sp. GB	Banyuls, France	AF474287 a	–	–
Pionosyllis augeneri Hartmann-Schröder, 1979	Sydney, Australia	EF123832	–	EF123794
Pionosyllis compacta Malmgren, 1867	Trondheim, Norway	EF123885	–	–
Pionosyllis enigmatica (Wesenberg-Lund, 1950)	Tjärno, Sweden	EF123826	EF123758	EF123795
Pionosyllis lamelligera Saint-Joseph, 1887	Port de la Selva, Girona, Spain	EF123864	EF123759	EF123796
Proceraea aurantiaca Claparède, 1868 GB	Banyuls, France	AF474324 a	–	AF474278 a
Proceraea okadai (Imajima, 1966) GB	Washington, USA	AF474319 a	–	AF474273 a
Proceraea picta Ehlers, 1864	Banyuls, France	EF123854	EF123760	–
Proceraea picta GB	Banyuls, France	AF474317 a	–	AF474271 a
Procerastea sp. GB	California, USA	AF474315 a	–	AF474269 a
Prosphaerosyllis sp.	Port de la Selva, Girona, Spain	EF123881	EF123761	EF123797
Prosphaerosyllis xarifae Hartmann-Schröder, 1960	Galicia, Spain	EF123836	–	–
Salvatoria clavata (Claparède, 1863)	Port de la Selva, Girona, Spain	EF123825	–	–
Salvatoria koorineclavata San Martín, 2005	Sydney, Australia	EF123835	–	–
Salvatoria limbata (Claparède, 1868)	Port de la Selva, Girona, Spain	EF123872	–	–
Salvatoria limbata GB	Koster Area, Sweden	AF474289 a	–	–
Sphaerosyllis austriaca Banse, 1959	Port de la Selva, Girona, Spain	EF123884	EF123763	EF123799
Sphaerosyllis bardukaciculata San Martín, 2005	Sydney, Australia	EF123842	EF123764	–
Sphaerosyllis boeroi Musco, Çinar and Giangrande, 2005	Port de la Selva, Girona, Spain	EF123856	–	EF123800
Sphaerosyllis densopapillata Hartmann-Schröder, 1979	Sydney, Australia	EF123879	–	–

Within Syllinae, there were two principal monophyletic groups. The first was well supported (98SR; 23B) containing *Eurysyllis* Ehlers, 1864 and *Trypanosyllis* Claparède, 1864 species. The second, less well supported (41SR, 10B), included *Geminosyllis ohma* (Imajima, 1966), and was the sister group of another clade containing species of *Syllis*, *Opisthosyllis* Langerhans, 1879, *Branchiosyllis* (Gravier, 1900) and *Haplosyllis* Langerhans, 1879 species (4B). The present analysis suggests that the large genus *Syllis* is paraphyletic. *Branchiosyllis* and *Haplosyllis* species derive from a paraphyletic *Syllis*.

Discussion

This study includes 57 more nominal taxa over previous molecular data sets devoted to consideration of syllid polychaetes. The resulting phylogenetic hypothesis shows Syllidae as a monophyletic group, though support values are still not very high. Within Syllidae most groups found to be monophyletic by Nygren and Sundberg (2003) also were recovered. These include Autolytinae, Syllinae and Exogoninae, though Exogoninae is still poorly supported. Eusyllinae, in contrast, is paraphyletic.

The genera *Syllides*, *Astreptosyllis* and *Streptosyllis* were in a distinct group (Clade I) sister to the rest of Syllidae. This Clade II, comprising the rest of the selected genera, is a well-defined, strongly supported group. The molecular results suggest that *Brania* and *Sphaerosyllis* could be paraphyletic, while the situation for *Odontosyllis*, *Prosphaerosyllis* and *Erinaceusyllis* is not clear. The genera *Pionosyllis* and *Syllis* are clearly paraphyletic (or polyphyletic) and need reorganization. The *Syllis* species complexes proposed by Licher (1999) are without phylogenetic support. The genera *Branchiosyllis* and *Haplosyllis* each are derived within the genus *Syllis*. The genus *Proceraea* Ehlers, 1864 may be paraphyletic. The phylogenetic relationships found here for Sphaerodoridae are interesting as the position of the group has not previously been well elucidated (Rouse and Fauchald, 1997; Pleijel and Dahlgren, 1998; Rouse, 1999, 2000). The topology of the depicted consensus suggests that the genus *Sphaerodoropsis* Hartman & Fauchald, 1971 is a monophyletic group distinct from Syllidae. Sphaerodoridae shares several morphological similarities with Syllidae (Fauchald and Rouse, 1997), the most remarkable being the presence of a proventricle feeding apparatus (Aguado and Rouse, 2006). One of the outgroup taxa selected herein, *Sphaerodoropsis anae*, possess a clear and obvious proventricle (Aguado and Rouse, 2006). A similar structure has been found in other families, such as Nautilinielidae and Pilargidae (Rouse and Pleijel, 2001). The results presented herein, and that the proventricle is found in other families, together suggest convergence or an appearance in a distant ancestor with multiple reversals. Either scenario implies that the presence of a proventricle in Syllidae should not be considered the defining unique unreversed synapomorphy for the group (*contra* Glasby, 1993). The digestive tube of syllids was studied by Haswell (1886, 1921) and more recently by Delgado et al. (1992). Detailed histological comparisons of similar features in other groups may differentiate structures that are otherwise externally indistinguishable.

Within Syllidae, the genera *Syllides*, *Astreptosyllis*, *Streptosyllis* and *Streptospinigera* have been thought to be related to each other in sharing some peculiar morphological characters, e.g., the complex shape of compound chaetae and aciculae (excepting *Syllides*) and a similar articulation pattern for antennae, tentacular and dorsal cirri (San Martín, 2003). Our results corroborate the hypothesis of Licher (1999) in finding these genera as a basal monophyletic group apart from the rest of Syllidae. Though monophyletic, their association with the remainder of the Syllidae is weak (SR = 43) perhaps because 18S rDNA were not available for *Astreptosyllis* or *Streptosyllis* species. Additional taxa and sequence data should be acquired so as to test their monophyly with Syllidae and to better determine the relationships in Clade I.

Most of the syllid genera found to be monophyletic in Clade II share the presence of a chitinous tooth in the pharynx. Glasby (1993) and Fauchald and Rouse (1997) considered this structure to be homologous with the jaws present in other groups of Phyllodocida (e.g., Nereididae, Pisionidae, Chrysopetalidae and Polynoidae). However, on the basis of histological comparisons, Purschke (1988) found that a typical cuticle composed the tooth, whereas jaws were denser structures with a non-chitinous composition. Within Syllidae, the pharingeal tooth is present in nearly all species of Exogoninae and Syllinae [excepting some genera, e.g., *Inermosyllis* San Martín, 2003 and *Xenosyllis* Marion & Bobretzky, 1875, neither of which was available for this study] and most of the genera traditionally included in Eusyllinae (excepting the genera *Streptosyllis*, *Astreptosyllis*, *Streptospinigera*, *Syllides*, *Anoplosyllis* Claparède, 1868, *Odontosyllis*, and *Amblyosyllis*). Nor is the tooth present in Autolytinae. If the pharyngeal tooth is not homologous with jaws, it could have arisen in the common ancestor for Clade II, later disappearing in various groups.

The topology of clade II agrees with the result of Nygren and Sundberg (2003) and Nygren (2004) in terms of monophyly of Autolytinae, Syllinae and Exogoninae. In the consensus of their combined data set, Nygren and Sundberg (2003) found Autolytinae as sister group to Exogoninae, Syllinae and some genera of Eusyllinae. That study included only 12 non-autolytine

Table 2
(*Continued*)

Taxon	Locality	GenBank accession no.		
		18S	CO-I	16S
Sphaerosyllis glandulata Perkins, 1981	Port de la Selva, Girona, Spain	EF123840	EF123765	–
Sphaerosyllis hirsuta Ehlers, 1897	Sydney, Australia	EF123870	–	–
Sphaerosyllis hystrix Claparède, 1863	Port de la Selva, Girona, Spain	EF123880	–	–
Sphaerosyllis pirifera Claparède, 1868	Port de la Selva, Girona, Spain	EF123845	EF123766	–
Sphaerosyllis sp.	Port de la Selva, Girona, Spain	EF123853	EF123767	EF123801
Sphaerosyllis taylori Perkins, 1981	Port de la Selva, Girona, Spain	EF123866-7	–	–
Streptosyllis bidentata Southern, 1914	Port de la Selva, Girona, Spain	–	EF123768	EF123802
Syllides convolutus Webster and Benedict, 1884	Port de la Selva, Girona, Spain	EF123829-30	EF123769	EF123803
Syllides fulvus (Marion and Bobretzky, 1875)	Banyuls, France	EF123839	EF123770	EF123804
Syllis amica Quatrefages, 1865	Galicia, Spain	–	–	EF123821
Syllis armillaris (O.F. Müller, 1771) GB	Kaldbak, Faroe Islands	AF474292 a	–	–
Syllis columbretensis (Campoy, 1982)	Port de la Selva, Girona, Spain	–	EF123771	EF123805
Syllis compacta Gravier, 1900	Altea, Spain	EF123846-7	EF123772	EF123806
Syllis corallicola Verrill, 1900	Port de la Selva, Girona, Spain	EF123875	–	EF123807
Syllis ehlersioides (Marenzeller, 1890)	Manazuru Peninsula, Japan	EF123841	EF123773	EF123808
Syllis ferrani Alós and San Martín, 1987	Port de la Selva, Girona, Spain	EF123874	EF123775	EF123809
Syllis garciai (Campoy, 1982)	Galicia, Spain	EF123869	EF123776	–
Syllis gerlachi (Hartmann-Schröder, 1960)	Port de la Selva, Girona, Spain	–	EF123777	EF123810
Syllis gracilis Grube, 1840	Galicia, Spain	EF123876	EF123778	EF123811
Syllis hyalina Grube, 1863	Port de la Selva, Girona, Spain	EF123851-2	EF123779	EF123818
Syllis krohni (Ehlers, 1864)	Azores Islands, Portugal	EF123859	–	EF155920
Syllis lutea (Hartmann-Schröder, 1960)	Sydney, Australia	EF123865	–	–
Syllis marugani Aguado, San Martín and Nishi, 2006	Manazuru Peninsula, Japan	EF123862-3	EF123780	EF123812
Syllis monilata (Imajima, 1966)	Manazuru Peninsula, Japan	EF123860-1	EF123781	EF123819
Syllis nipponica (Imajima, 1966)	Manazuru Peninsula, Japan	–	EF123782	EF123813
Syllis okadai Fauvel, 1934	Manazuru Peninsula, Japan	EF123857-8	EF123783	EF123814
Syllis pigmentata (Chamberlin, 1919)	Manazuru Peninsula, Japan	EF155921	EF123774	–
Syllis variegata Grube, 1860	Galicia, Spain	–	–	EF123822
Syllis vivipara Krohn, 1869	Galicia, Spain	EF123848-9	–	EF123815
Syllis westheidei San Martín, 1984	Port de la Selva, Girona, Spain	EF123877	EF123784	–
Trypanosyllis coeliaca Claparède, 1868	Port de la Selva, Girona, Spain	EF123878	EF123785	EF123816
Trypanosyllis zebra (Grube, 1860)	Banyuls, France	–	EF123786	EF123817
Virchowia clavata Langerhans, 1879 GB	Banyuls, France	AF474314 a	–	AF474268 a
Outgroups				
Ceratonereis longiceratophora Hartmann-Schröder, 1985 GB	b: Hawkesbury R. c: Genbank	AB106251 b	AY583701 c	–
Chrysopetalidae sp GB	Santa Catalina Island, California, USA	AY176284 d	–	–
Eunice pennata (Müller, 1776) GB	e: Koster Area, Sweden f: Genbank	AY040684 f	–	AF321418 e
Harmothoe imbricata (Linnaeus, 1767) GB	Sweden	AY340434 g	AY839580 j	AY340463 g
Hesiospina sp GB	Madang, Papua New Guinea	AY340435 h	–	AY340464 g
Lepidonotus squamatus (Linnaeus, 1758) GB	Bohuslän, Sweden	DQ779656 g	DQ779620 g	–
Nereis pelagica Linnaeus, 1758 GB	Genbank	AY340438 g	–	AY340470 g
Paralepidonotus ampuliferus (Grube, 1878) GB	Genbank	AF519237 i	AY583698 c	–
Phyllodoce maculata (Linnaeus, 1767) GB	Koster Area, Sweden	AY176302 d	AY839586 j	–
Pisione remota (Southern, 1914) GB	j: Gullmarsfjord, Sweden k: Banyuls, France	AY839574 j	AF221575 k	–
Sigalion bandaensis Horst, 1917 GB	Genbank	AB106254 b	AY583699 c	–
Sigambra sp GB	Japan	AY340444 g	–	AY340481 g
Sphaerodoropsis anae Aguado and Rouse, 2006	Easter Island	EF123871	EF123762	EF123798
Sphaerodoropsi philippi (Fauvel, 1911) GB	Koster Area, Sweden	AY176307 d	–	–
Sthenelais boa (Johnston, 1833) GB	g:Brittany, France j: Sweden	DQ779672 g	AY839587 j	–

70–95% ethanol, identified by the first author and maintained at 4 °C until use for DNA extraction. The posterior half of each specimen was used for DNA extraction in order to maintain the ability to later confirm the identity of the species. Extractions of the smallest specimens were made using whole worms. Anterior parts of the larger specimens are currently located at the Museo Nacional de Ciencias Naturales de Madrid (MNCNM), the Australian Museum (AM) and the South Australian Museum (SAM).

A total of 88 species of syllids were included as the ingroup: 66 were collected during 2003–05 from different localities specifically for this study (Table 2) and 22 were downloaded from GenBank. Outgroup taxa included 15 species of Eunicidae, Sphaerodoridae, Polynoidae, Sigalionidae, Pisionidae, Nereididae, Chrysopetalidae, Pilargidae and Hesionidae (Tables 1 and 2), all of which were downloaded from GenBank with the exception of *Sphaerodoropsis anae* (Aguado and Rouse, 2006).

DNA extraction, purification and amplification

DNeasy Tissue Kit (Qiagen, Valencia, CA, USA) was used for tissue lysis and DNA purification. Polymerase chain reaction (PCR) amplification of nuclear 18S rDNA and mitochondrial 16S rDNA and cytochrome *c* oxidase subunit I (CO-I) was accomplished with the primers listed in Table 3. Two sets of different primers pairs were used for 18S: "1F5R", "3FBI", "A2.09R" (Rousset et al., 2007) and "AL", "CY", "BO" (Apakupakul et al., 1999; Borda and Siddall, 2004). In each case, three overlapping fragments were obtained of approximately 600 bp. Amplifications of 16S and CO-I yielded fragments of approximately 600 and 650 bp, respectively. Amplification reaction mixtures for gene fragments used Ready-To-Go™ PCR Beads (Amersham Pharmacia Biotech, Piscataway, NJ, USA), 0.5–1 μL of each primer, 1 μL DNA template and 22–23 μL RNase-free H_2O (total volume, 25 μL). Amplification reactions were performed in an Eppendorf Mastercycler.

Different annealing and extension temperatures were used depending on the gene and the taxon, being the lowest for CO-I. The following amplification protocol was used: heated to 94 °C for 5 min, followed by 34–39 cycles of 94 °C (20–30 s), 45–50 °C (15–30 s), and 68–72 °C (45 s) and a final extension at 72 °C (7 min). Polymerase chain reaction products were visualized on 2% agarose gels containing ethidium bromide. Some PCR products were amplified again diluting 4 μL of product in 10–20 μL RNase-free H_2O; the same amplification protocol was used with 0.5 μL of each (10 mM) primer, 5 μL of DNA and 19 μL RNase-free H_2O (total volume, 25 μL). The ArrayIt PCR Purification Kit protocol (TeleChem International, Sunnydale, CA, USA) and AMPure Purification system PCR Cleaning protocol (Wheeler Protocols) were employed to purify amplification products.

DNA sequencing

Amplification products were sequenced in both directions. Each sequencing reaction mixture, including 1 μL BigDye (Applied Biosystems, Perkin-Elmer Corporation, Foster City, CA, USA), 1 μL of each (1 mM) primer (single primer for each direction), and 3 μL of DNA template, heated to 96 °C for 5 min, ran for 35 cycles of 96 °C (30 s), 50 °C (30 s) and 60 °C (4 min). Sequences were purified by ethanol precipitation to remove primers and unincorporated dyes or by following the CleanSEQ protocol (BigDye removal system, Wheeler protocols). Products were re-suspended in at least 6 μL of formamide and electrophoresed in an ABI Prism 3730 sequencer (Applied Biosystems, Perkin-Elmer Corporation).

DNA-sequence alignment

Sequences of complimentary strands were edited and reconciled using Sequence Navigator (Applied Biosystems) and CodonCode Aligner (CodonCode, Dedham,

Table 3
Primers used for PCR amplification and sequencing

Gene	Primer name	Primer sequence	Reference
Nuclear			
18S rDNA	A	5′-AACCTGGTTGATCCTGCCAGT-3′	Medlin et al. (1988)
	L	5′-CCAACTACGAGCTTTT-3′	Apakupakul et al. (1999)
	C	5′-CGGTAATTCCAGCTC-3′	Apakupakul et al. (1999)
	Y	5′-CAGACAAATCGCTCC-3′	Apakupakul et al. (1999)
	B	5′-TGATCCTTCCGCAGGTTCACCT-3′	Medlin et al. (1988)
	O	5′-AAGGGCACCACCAG-3′	Apakupakul et al. (1999)
	1F	5′-TACCTGGTTGATCCTGCCAGTAG-3′	Rousset et al. (2007)
	5R	5′-CTTGGCAAATGCTTTCGC-3′	Rousset et al. (2007)
	3F	5′-GTTCGATTCCGGAGAGGGA-3′	Rousset et al. (2007)
	BI	5′-GAGTCTCGTTCGTTATCGGA-3′	Rousset et al. (2007)
	A2.0	5′-ATGGTTGCAAAGCTGAAAC-3′	Rousset et al. (2007)
	9R	5′-GATCCTTCCGCAGGTTCACCTAC-3′	Rousset et al. (2007)
16S rDNA			
	A	5′-CGCCTGTTTATCAAAAACAT-3′	Simon et al. (1994)
	B	5′-CTCCGGTTTGAACTCAGATCA-3′	Simon et al. (1994)
Mitochondrial			
CO-I	LCOI1490	5′-GGTCAACAAATCATAAAGATATTGG-3′	Folmer et al. (1994)
	HCOI2198	5′-TAAACTTCAGGGTGACCAAAAAATCA-3′	Folmer et al. (1994)

MA, USA). Some fragments of 18S were reconciled using Genejockey II (Biosoft, Oxford, UK). Alignments of the two mitochondrial and the nuclear genes were accomplished using Clustal X version 1.83 (Thompson et al., 1997) with gap open value of 12 and gap extension cost of 6. Alignment was subsequently manually edited by eye using MacClade (Maddison and Maddison, 2001). Following preliminary analyses using all sites, which resulted in overall poor support, as well as paraphyletic Autolytinae and Syllinae each without jackknife support, gap positions and regions that could not be unambiguously aligned were excluded from the analysis; these included 555 of 2156 sites in 18S, 111 of 542 sites in 16S. Altogether, 1328 nucleotide positions were parsimony informative in the combined analysis.

Phylogenetic analyses

Parsimony analysis was performed in PAUP* 4.0b10 (Swofford, 2002) in combination with PAUPRat "PAUP* implementation of the parsimony ratchet" (Nixon, 1999), beta version 1 (Sikes and Lewis, 2001). Each ratchet analysis was run for 3000 replicates with default settings. The analysis was also performed in TNT (Goloboff et al., 2004) using sectorial searches, ratcheting and tree fusing algorithms, the results of which were submitted back to TNT for TBR branch swapping. All characters were left unweighted and non-additive. Bremer support values (B, see Bremer, 1988) and Symmetric Resampling frequencies (SR, see Goloboff et al., 2003) also were generated with TNT. The strict consensus and branch lengths were plotted with PAUP.

Data on reproductive modes

Reproductive mode for each syllid species was assessed from original descriptions: San Martín (2003), and more specifically in San Martín (2005) for Exogoninae; San Martín and Hutchings (2006) for Eusyllinae; Licher (1999) and Imajima (1966) for Syllinae; as well as Gidholm (1965), Hamond (1967), Nygren (1999, 2004), Okada (1933, 1937), Berkeley (1923), Cognetti (1953) and Dehorne (1917) for Autolytinae. Additional inferences were based on direct observations of the studied material. When it was unknown, the reproductive system for other species of the genus has been assumed. Brooding in *Syllides fulvus* (Marion & Bobretzky, 1875) and *Syllides convolutus* Webster & Benedict, 1884 has never been shown; however, it has been observed in other species of the genus therefore they are shown in Fig. 1 as ventral brooders. There is no reference about brooding in any species of *Virchowia* Langerhans, 1879, consequently *Virchowia clavata* Langerhans, 1879 is not shown in Fig. 1 as a possible brooder, although it may carry ventral egg sacs as the rest of Autolytinae. The only species in a genus with an unknown reproduction system is *Geminosyllis ohma* (Imajima, 1966), and here it has been considered schizogamic due to its placement within Syllinae.

Results

Parsimony analysis performed in PAUPratchet yielded 18 equally parsimonious trees with 11 373 steps (RI: 0.5 and CI: 0.3). Analysis performed in TNT yielded 306 trees at 11 373 steps. The strict consensus of trees calculated in TNT is shown in Fig. 1. The resulting cladogram from the combined data showed that Syllidae is a monophyletic group, although the support values were simultaneously high (17B) and low (43SR). The consensus showed that within Syllidae there are two well supported clades. Clade I contained species of *Syllides*, *Streptosyllis* and *Astreptosyllis* (100SR, 17B) and Clade II contained the rest of the included species (91SR; 17B). In the first clade, *Syllides convolutus* was sister to *Streptosyllis bidentata* Southern, 1914 (41SR; 8B) as opposed to *Syllides fulvus*. Clade II was secondarily divided into two monophyletic groups. The first was supported by a SR value of 65 (3B) and comprised *Amblyosyllis* Grube, 1857 and *Dioplosyllis* Gidholm, 1962 species (98SR; 8B) joined to another clade containing most of the species traditionally classified as Eusyllinae (14SR, 3B), and Autolytinae genera (100 SR; 20B). *Amblyosyllis formosa* (Claparède, 1863) was sister to *Dioplosyllis* sp. (56SR; 5B) as opposed to *Amblyosyllis* sp. *Pionosyllis* Malmgren, 1867 and *Odontosyllis* Claparède, 1863 were paraphyletic groups. Specimens of *Odontosyllis gibba* Claparède, 1863, *Nudisyllis pulligera* and *Eusyllis blomstrandi* Malmgren, 1867 newly selected for this study each appeared to be adjacent to the same species downloaded from GenBank and in well supported clades. Autolytinae was strongly supported, as were the included genera *Epigamia* (100SR; 18B) and *Myrianida* Milne Edwards, 1845 (100SR; 21B).

The second major group within Clade II, like the first, was well supported (63SR, 3B) and was secondarily divided into two clades corresponding to the classical subfamilies Syllinae (59SR, 9B) and Exogoninae (to which *Pionosyllis augeneri* was sister) (33SR; 3B). Within Exogoninae, *Salvatoria* was a monophyletic group (36SR, 1B) but *Brania* and *Sphaerosyllis* appear to be paraphyletic. *Erinaceusyllis* species were not each others' closest relatives, nor were the included *Prosphaerosyllis* species. *Exogone naidina* Örsted, 1845, newly included in this study, was adjacent to the same species obtained from GenBank. However, *Salvatoria limbata* (Claparède, 1868), newly sequenced for this study, seemed to be closer to *Salvatoria clavata* (Claparède, 1863) than to the *S. limbata* from GenBank.

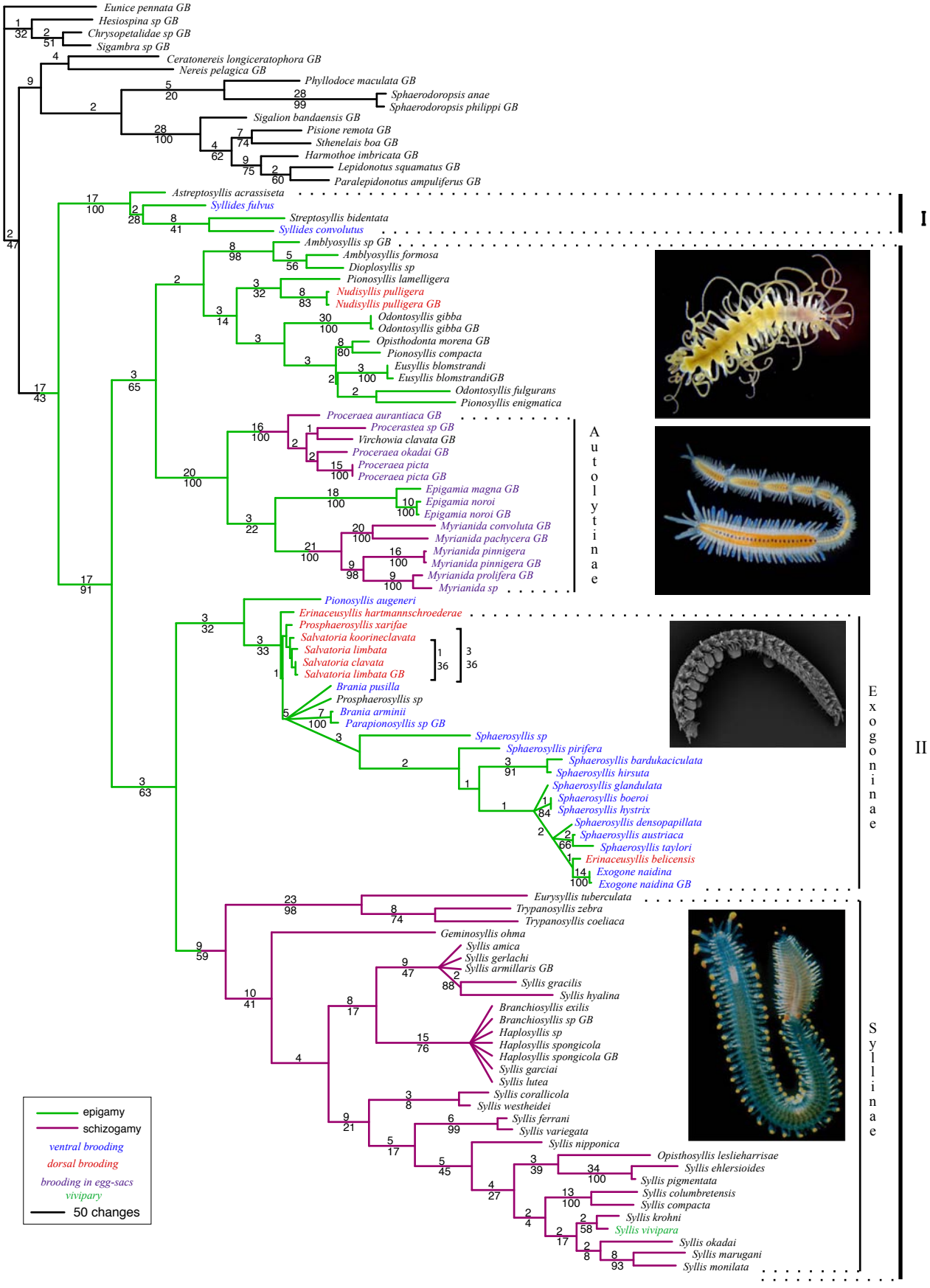

Fig. 1. Strict consensus tree of the combined data set. Below nodes (where they occur) are the symmetric resampling values; above nodes are the bremer support values. Branches are drawn proportional to amount of change save for those involved in polytomies. GB: from GenBank. Pictures from top to bottom: *Amblyosyllis* sp. courtesy of G. Rouse, *Myrianida pachycera* (Augener, 1913), courtesy of G. Rouse, *Sphaerosyllis hirsuta* Ehlers, 1897 courtesy of G. San Matín, Syllinae with stolon courtesy of G. Rouse.

syllids. Our results suggest instead that most of the genera of the classic Eusyllinae are more closely related to Autolytinae than they are to Syllinae or Exogoninae. Lack of monophyly for Eusyllinae has been anticipated by previous authors (Glasby, 1994; San Martín, 2003; San Martín and Hutchings, 2006) albeit without the benefit of a phylogenetic tree. This study corroborates the notion that *Pionosyllis* is polyphyletic. The genus is very much in need of phylogenetic revision because it is one of the largest and most complex in Syllidae, with more than 40 species, and spans considerable differences in morphological characters.

Either *Amblyosyllis* is a paraphyletic genus or *Dioplosyllis* is a junior synonym. Both genera are quite similar in numerous morphological features. At present only a partial sequence of 18S rDNA could be included for *Dioplosyllis* sp. More data are required to assess the relationships within and among *Amblyosyllis* species. Within Exogoninae, *Erinaceusyllis belicensis* (Russell, 1989) also is represented by only a partial sequence of 18S rDNA perhaps leaving its placement as the sister group of *Exogone* as unstable.

Among *Syllis* species, seven of the complexes proposed by Licher (1999) are represented by taxa included in our analyses. Five of those species complexes were represented here by more than one species: *Syllis corallicola* Verrill, 1900, *S. monilata* (Imajima, 1966) and *S. nipponica* (Imajima, 1966) from the *corallicola* complex; *Syllis pigmentata* (Chamberlin, 1919) and *Syllis okadai* Fauvel, 1934 from the *vittata* complex; *Syllis amica* Quatrefages, 1865 and *Syllis ferrani* Alós & San Martín, 1987 from the *amica* complex; as well as *Syllis vivipara* Krohn, 1869 and *Syllis gerlachi* (Hartmann-Schröder, 1960) from the *prolifera* complex; whereas *Syllis armillaris* (O.F. Müller, 1771), *Syllis hyalina* Grube, 1863 and *Syllis krohni* Ehlers, 1864 represented the *armillaris* complex (Licher, 1999). None of the species complexes proposed by Licher (1999) for which we had more than one representative was supported herein as a monophyletic group. Neither do the proposed phylogenetic relationships among species complexes suggested by Licher (1999) find any support in our results. *Syllis armillaris*, *S. hyalina* and *S. gracilis* (together forming a monophyletic group here) have the same dorsal cirri and anterior chaetae and have been previously considered to be a complex of closely related species (San Martín, 2003; Musco and Giangrande, 2005). Relationships suggested by Aguado et al. (2006) between *Syllis marugani* Aguado, San Martín & Nishi, 2006 and similar species (included in the clade comprising *S. krohni* and *S. monilata*) were corroborated. *Haplosyllis* and *Branchiosyllis* species appear to have evolved from a common ancestor within *Syllis* species. In both, the shape of chaetae is at odds with the common pattern among syllids, which may be modifications related to a symbiotic way of life (Martin and Britayev, 1998). *Opisthosyllis* may also have derived from within the genus *Syllis*. More species of this genus are necessary to test monophyly and relative relationships among *Syllis*-*Opisthosyllis* species.

The resulting cladogram fully corroborates the hypotheses of Nygren (1999) and Nygren and Sundberg (2003) regarding reproductive modes. Epigamy is hypothesized to be the plesiomorphic condition with schizogamy appearing twice in Autolytinae and Syllinae as distinct events. In Autolytinae, schizogamy could have appeared once, reversing in *Epigamia,* or it could have appeared independently in *Myrianida* and *Proceraea–Procerastea–Virchowia* clades (Fig. 1), both being equally parsimonious possibilities.

Hypotheses regarding dorsal and ventral brooding among the Exogoninae also were corroborated. *Erinaceusyllis*, *Prosphaerosyllis* and *Salvatoria* are dorsal brooders, whereas *Exogone*, *Parapionosyllis*, *Sphaerosyllis* and *Brania* are ventral brooders. *Erinaceusyllis belicensis* as the sister group of *Exogone* was considered above to be potentially awkward. *Prosphaerosyllis* sp. was previously identified as *Sphaerosyllis* sp. by San Martín (2003). Regardless of these peculiarities, dorsal brooding could easily be the ancestral state for Exogoninae perhaps as an adaptation to interstitial life as suggested by Westheide (1984, 1987), later changing to ventral brooding. Whether brooding in *Pionosyllis augeneri*, the apparent sister group to Exogoninae, is similarly derived is difficult to assess because development of embryos has never been observed. Brooding in *Syllides* and *Nudisyllis pulligera* is clearly unrelated to that in the Exogoninae. A connection with the nephridial pore has not been demonstrated among species of *Syllides*, and eggs are attached to dorsal cirri of *N. pulligera*, not to the notochaetae. Inclusion of *Nooralia* in future analyses would be valuable so as to clarify the relationship of a third kind of brooding system in which eggs are attached to compound neurochaetae. Parental care in Autolytinae, in which the female cares for the young in one or several egg sacs, also seems to be a separate evolutionary event unrelated to the other types of brooding by syllids. Viviparity is present only in one of the terminal taxa selected for this study, *S. vivipara*, appearing as an individual phenomenon derived from schizogamy.

The phylum Annelida remains one for which the basic relationships of taxonomic groups have yet to be fully elucidated notwithstanding the size of the phylum and the ubiquity of its constituents. Unlike tree-of-life scale studies well underway for arthropod groups and mollusks, deep annelid phylogenetics is only now emerging from reliance on single-locus analyses for large groups or restriction to exemplars wherein multiple loci are used. Already, though, it appears that large-scale multilocus phylogenetic analyses, such as this study, and all-Annelida analyses (e.g., Rousset et al.,

2007) may be limited by the information content available in rDNA and mitochondrial loci often used for arthropods—a problem that may be ameliorated by the development of novel loci, or other kinds of data from EST libraries.

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Phylogeny of Syllidae (Phyllodocida, Annelida) based on morphological data

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ABSTRACT

The phylogeny of Syllidae is assessed in two parsimony analyses of 111 morphological characters. The first analysis included one species of each 64 valid genera of the family, as well as members of other families of Phyllodocida. In the second analysis 19 genera poorly known were excluded. Character information is based on examination of available types, additional non-types and newly collected material. Both analyses supported three of the four subfamilies (Exogoninae, Syllinae and Autolytinae) as monophyletic, poorly supported in the first analysis, while Eusyllinae was clearly a paraphyletic group. The monophyly of the family still needs to be demonstrated. Our results indicated high levels of homoplasy in the traditionally used morphological characters for the group. Considering the reproductive modes, schyzogamy might have appeared twice in the family as the derived condition from epigamy, and Exogoninae might be divided in two monophyletic groups attending to the brooding system. Results are compared with those from previous studies and with the most recently published phylogenetic analysis of Syllidae based on molecular data from nuclear 18S rDNA and mitochondrial 16S rDNA and cytochrome *c* oxydase subunit I.

INTRODUCTION

Syllidae is a highly diverse family with more than 60 genera, 700 species, and a difficult taxonomy. There are numerous studies about the group; however, a synthetic and comprehensive study embracing the whole family is still lacking (Pleijel, 2001a). The family is currently divided into four subfamilies: Syllinae Grube, 1850; Exogoninae Langerhans,

1879; Eusyllinae Malaquin, 1893, and Autolytinae Langerhans, 1879 (Fauchald, 1977; San Martín, 2003). The main diagnosis characters that have been traditionally used to characterize and differentiate each subfamily are detailed in Table 1. However, there are numerous exceptions for each character.

Syllids are easily recognized because all of them have a proventricle, which is often visible by transparency. The proventricle is a differentiation of the digestive tube, which is supposed to work as a suctorial bomb in the feeding processes (Fauchald & Jumars, 1979; San Martín, 2003). It has been considered the synapomorphy of the group by some authors (Fauchald & Rouse, 1997; Glasby, 1993), but it is also present in other families such as Sphaerodoridae (Aguado & Rouse, 2006).

Syllids exhibits some of the most spectacular specializations in reproduction (Pleijel, 2001a). There are two distinct reproductive modes: epigamy and schyzogamy. Both modes imply strong changes in the body and behaviour. The principal difference between them is that these changes affect to the whole individual in epigamy, while in schizogamy these changes occur only in the stolons, which are developed by the posterior part of the body. In the epigamic condition, the animal develops swimming noto-chaetae and increases the size of eyes and cephalic appendages. In the schyzogamic condition stolons with swimming noto-chaetae, large eyes and long cephalic appendages are developed and later dettached from the anterior part. There are two types of schyzogamy: gemmiparity, where a series of several stolons is produced, and scissiparity, where a single stolon appears. In these two reproductive modes, the epigamic specimens (epitokes) and the delopped stolons (male and females, respectively) actively swim and releases oocytes and sperm. A special kind of schyzogamy has been reported in some species of *Trypanosyllis* Claparède, 1864, which develop several stolons but all of them attached at the same point (Schroeder & Hermans, 1975). Another species, which develops lateral buddings is *Syllis ramosa* McIntosh, 1879; it has a body divided in multiple branches which penetrate in the canal system of the host sponges, each of them forming stolons (Pleijel, 2001a). A special kind of epigamy has been reported in *Epigamia* Nygren, 2004 in which, during the reproductive transformation, the specimen also experiences the disintegration of pharynx and proventricle (Nygren, 2004). These distinct differences in reproduction of syllids have been widely studied (Malaquin, 1893; Potts, 1911;

Garwood, 1991; Franke, 1999; Nygren, 1999; 2004; Glasby, 2000; San Martín, 2003; Pleijel & Rouse, 2006). However, there are still many species and genera for which their reproduction remains unknown.

Epigamy has also been reported in other families of polychaetes (Nereididae, Phyllodocidae, Glyceridae, Scalibregmidae, Nephtyidae, Spionidae, Amphinomidae, Eunicidae and Opheliidae), although their morphological changes are not identical to those occurring in syllids (Rouse and Pleijel, 2001). Schyzogamic has been also reported for the genus *Palola* Gray, 1847 (Eunicidae) and some Phyllodocida (Pleijel & Rouse, 2006) but the process is remarkably different since there are no structural modifications in the stolons (Schoeder & Hermans, 1975).

In the family Syllidae, there are also different egg brooding modes. In Exogoninae, there are two different brooding care systems: dorsal brooding, where eggs are attached to dorsal notochaetae of the parental body; and ventral brooding, where the parental carry eggs in a ventral position attached to the nephridial pore. Some members of Eusyllinae display some variations of these brooding systems carrying eggs attached to dorsal cirri, or in ventral position, although the conexion with the nephridial pore has not been demonstrated (Heacox and Schroeder, 1978, 1979; Pierantoni, 1905; San Martín, 2003; Aguado *et al.*, 2007). Other brooding systems such as brooding in gelatinous masses and in ventral sacs have been reported for some species of Eusyllinae and Autolytinae, respectively (Pernet, 1998; Cognetti-Varriale, 1971). Finally, some species of Syllinae and Exogoninae are viviparous (Franke, 1999, San Martín, 2003; Pleijel and Rouse, 2006). Viviparity is considered an adaptation to the interstitial life more than a strategy characteristic of some genera (Westheide, 1984, 1987; Ding *et al.*, 1998). Garwood (1991) suggested that the pattern of reproductive modes in Syllidae might support the monophyly of the classical subfamilies.

The family is currently placed within Phyllodocida (Rouse and Fauchald, 1997; Rouse and Pleijel, 2001), which is a clade containing a large number of families, some of them still missplaced and others distributed in two groups: Aphroditiformia and Nereidiformia (Pleijel and Dahlgren, 1998). The latter contains Syllidae together with Chrysopetalidae, Hesionidae, Nautilienidae, Nereididae and Pilargidae. Several previous phylogenetic studies on

Phyllodocida have been done. Glasby (1993) performed a cladistic analysis including the families of Nereidoidea (s. Hartmann-Schröder, 1985); relationships within the genus *Phyllodoce* Lamark, 1818 were dicussed by Pleijel (1993); Licher & Westheide (1994) studied the phylogenetic position of Pilargidae; Pleijel & Dahlgren (1995, 1998) considered the phylogenetic relationships between Chrysopetallidae and Hesionidae; Nereididae was firstly considered by Fitzhugh (1987) and later by Santos *et al.* (2005); and Hesionidae has been analysed by Pleijel (1998, 1999, 2001b) and more recently by Ruta *et al.* (2007), also including molecular data. The phylogeny of the family Syllidae has been previously assessed in some studies, although only partially (Licher, 1999, Nygren, 1999; Nygren and Sundberg, 2003; Nygren, 2004; and Aguado *et al.*, 2007).

Aguado *et al.* (2007) performed a phylogenetic study based on molecular data from nuclear 18S rDNA and mitochondrial 16S rDNA and cytochrome *c* oxydase subunit I. This study included the highest number of terminals until the moment, 88 syllids in the four classical subfamilies, but only representing 29 genera. Results of the parsimony analysis supported Syllidae as a monophyletic group, though not very consistently; the genera *Astreptosyllis* Kudenov and Dorsey, 1982, *Streptosyllis* Webster and Benedict, 1884 and *Syllides* Örsted, 1845 comprised a monophyletic group well differentiated from the rest of the Syllidae. The subfamilies Autolytinae, Syllinae and Exogoninae were monophyletic, though Exogoninae was not well supported, while Eusyllinae was clearly paraphyletic. Epigamy was found to be the plesiomorphic condition and schizogamy appeared independently in Autolytinae and Syllinae.

This study aims to represent a continuing effort to unveil the phylogenetic relationships among groups in Syllidae as well as to address whether the monophyly of the group is a reality. In addition, it aims at continuing to investigate the evolution of reproductive modes and some morphological characters traditionally used for diagnoses of the classical subfamilies and their genera. For these purposes we performed two different analyses, both based on the same morphological characters. The first one included one species of each valid genus in Syllidae, for the second analysis the number of taxa was reduced (excluding the genera that are monotypic and/or not well known) obtaining better resolution.

Subfamily	Ventral cirri	Palps	Antennae, "tentacular" and dorsal cirri	Nuchal organs	Reproduction
Eusyllinae	Present	Free or basally fused	Smooth and long	Ciliated grooves	Epigamy
Exogoninae	Present	Partially or totally fused	Smooth and short	Ciliated grooves	Epigamy dorsal and ventral brooding of eggs
Syllinae	Present	Free or basally fused	Articulated and long	Ciliated grooves	Schizogamy
Autolytinae	Absent	Fused and reduced	Smooth, long or short	Nuchal epaulettes	Schizogamy

Table 1. Diagnostic characters traditionally used to differentiate subfamilies within Syllidae.

MATERIAL AND METHODS

Material studied

Studied material has been loaned by the Museo Nacional de Ciencias Naturales de Madrid (MNCN); Zoologisches Institut und Zoologisches Museum, Universität Hamburg (ZMH); Zoologisch Museum, Universiteit van Amsterdam (ZMA); Muséum Nationale d´Histoire Naturelle, Paris (MNHN); Zoologisches Museum, Museum für Naturkunde der Humboldt-Universität, Berlin (ZMB); Australian Museum, Sydney (AM); Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt (FNS); Muzeum Przyrodnicze Wroclaw (MPW); Naturhistorisches Museum Wien (NMW); Vitenskapsmuseet, Norges Teknisk-Naturvitenskapelige Universitet, Trondheim (NTNU); Natural History Museum of London (NHML); The Smithsonian Institution, Washington (USNM); Natural History Museum of Los Angeles County (NHMLAC); South African Museum, Cape Town (SAM); Ege University, Faculty of Fisheries, Izmir (ESFM); the Kitakyushu Museum of Natural History and Human History, Fukuoka (KMNH); the Coastal Branch of Natural History Museum and Institute, Chiba (CBM); Universidad Autónoma de Nuevo León (UANL); and National Institute of Water and Atmosphere Research, Canterbury (NIWA).

The specimens were mostly preserved in 70% ethanol after fixation in formalin. Examinations were made using a compound microscope with interference contrast optics (Nomarsky). Drawings were made using a camera lucida drawing tube. Scanning Electron Microscope observations and photographs were made in the SIDI (Servicio Interdepartamental de Investigación) of the Universidad Autónoma de Madrid, Spain. Most of the pictures have been previously published elsewhere (see figure legends).

Selection of terminal taxa

Ingroup. In the first analysis we included terminals representing all the valid genera of the family, assuming that they are monophyletic. A total of 64 valid genera have been considered, although studies already in course and not finished are suggesting that this number should be increased. For instance, *Syllis* Lamarck, 1818, is the largest genus with more than 130 nominal species and it is supposed to be paraphyletic (Aguado *et al.,* 2007), and *Pionosyllis* is also a very large genus with more than 41 species and may be as well a paraphyletic group (Aguado *et al.,* 2007; San Martín, *et al.,* submitted a). However, phylogenetic studies focused in these problematic genera are not yet accepted for publication, and hence we decided not to include more than one species per each presently valid genus. The terminals and their current taxonomic situation are shown in Table 2. Character information was based on the examination of type and non-type specimens (since there was considerable missing information in some types), together with literature descriptions (Table 3). Nineteen genera were excluded for the second analysis (in green in Table 2) because they were not very well known, most of them monotypic, and hence scored with many question marks in the first analysis.

The genus *Calamizas* Ardwidsson, 1932 might be a member of Syllidae (Hartmann-Schröder, 1971; Glasby, 1993; Pleijel, 2001a), although other authors considered it as a different family (Fauchald, 1977; Hartmann-Schröder, 1996). Furthermore, it has not been included in our analysis since its description was incomplete and its morphology could be considerably modified by its parasitic condition.

Table 2. Genera and species included in the morphological analyses organized accoding to the traditional classification of family Syllidae (Fauchald, 1977; San Martín, 2003). Species in green were not included in the second analysis.

Annelida, Polychaeta

Phyllodocida

Family Pisionidae *Pisione longispinulata* Aguado & San Martín, 2004

Family Nereididae *Neanthes virens* (Sars, 1835)

Family Chrysopetalidae *Chrysopetalum maculata* Aguado, Capa & San Martín, 2003

Family Sphaerodoridae *Sphaerodoropsis anae* Aguado & Rouse, 2006

Family Syllidae Grube, 1850

Subfamily Syllinae Grube, 1850

Alcyonosyllis phili Glasby & Watson, 2001
Dentatisyllis mortoni Ding, Licher & Westheide, 1998
Eurysyllis tuberculata Ehlers, 1864
Trypanoseta ohma (Imajima & Hartmann, 1964)
Haplosyllides floridana Augener, 1924
Haplosyllis spongicola (Grube, 1855)
Inermosyllis balearica (San Martín, 1982)
Nuchalosyllis lamellicornis Rullier & Amoreux, 1979
Opisthosyllis brunnea Langerhans, 1879
Parahaplosyllis brevicirra Hartmann-Schröder, 1990
Parasphaerosyllis indica Monro, 1937
Plakosyllis brevipes Hartmann-Schröder, 1956
Rhopalosyllis hamulifera Augener, 1913
Syllis prolifera Krohn, 1852
Trypanosyllis aeolis Langerhans, 1879
Xenosyllis scabra (Ehlers, 1864)

Subfamily Exogoninae langerhans, 1879

Brania pusilla (Dujardin, 1851)
Cicese sphaerosylliphormis Díaz-Castañeda & San Martín, 2001
Erinaceusyllis serratosetosa (Hartmann-Schröder, 1972)
Exogone naidina Örsted, 1845
Nooralia bulgannabooyanga San Martín, 2002
Parexogone hebes (Webster & Benedict, 1884)
Parapionosyllis minuta (Pierantoni, 1903)
Proshaerosyllis xarifae (Hartmann-Schröder, 1960)
Salvatoria clavata (Claparède, 1863)
Sphaerosyllis hystrix Claparède, 1863

Subfamilia Autolytinae Langerhans, 1879

Epigamia labordai (San Martín & López, 2002)
Imajimaea zonata (Mohamed, 1973)
Levidorum hartmanae Perkins, 1987
Myrianida prolifera (Müller, 1788)
Pachyprocerastea hydrozoicola (Hartmann-Schröder, 1992)
Paraproceraea tamana (Imajima, 1966)
Paraprocerastea crocantinae San Martín & Alós, 1989
Planicirrata proceraeae (Hartmann-Schröder & Rosendfeld, 1990)
Procerastea halleziana Malaquin, 1893
Proceraea picta Ehlers, 1864
Virchowia clavata (langerhans, 1879)

Subfamily Eusyllinae Malaquin, 1893

Amblyosyllis speciosa Izuka, 1912
Anguillosyllis capensis Day, 1963
Anoplosyllis edentulus Claparède, 1868
Astreptosyllis acrassiseta Kudenov & Dorsey, 1982
Brachysyllis infuscata (Ehlers, 1901)
Pionosyllis weissmani Langerhans, 1879
Dioplosyllis cirrosa Gidholm, 1962
Eusyllis blomstrandi Malmgren, 1867
Nudisyllis pulligera (Krohn, 1852)
Odontosyllis fulgurans (Audouin & Milne Edwards, 1834)
Opisthodonta morena Langerhans, 1879
Palposyllis prosostoma Hartmann-Schröder, 1977

Paraehlersia ferrugina (Langerhans, 1881)
Paraopisthosyllis ornaticirra San Martín & Hutchings, 2006
Pionosyllis enigmatica (Wesenberg-Lund, 1950)
Psammosyllis wui Ding & Westheide, 1997
Streptodontha pterochaeta (Southern, 1914)
Streptospinigera heteroseta Kudenov, 1983
Streptosyllis websteri Southern, 1914
Syllides japonicus Imajima, 1966

Incertae sedis

Bollandia antipathicola Glasby, 1994
Clavisyllis alternata Knox, 1957
Lamellisyllis comans Day, 1960
Murrindisyllis kooromundrola San Martín, Aguado & Murray, 2007
Miscellania dentata Martín, Alós & Sardá, 1990
Neopetitia amphophthalma (Siewing, 1956)
Karroonsyllis exogoneformis San Martín & López, 2003

Outgroup. We have selected several terminals of close families to Syllidae, all of them pertaining to Phyllodocida and Nereidiformia (Rouse & Fauchald, 1997; Rouse & Pleijel, 2001). Four species each belonging to the families Nereididae, Pisionidae, Chrysopetallidae and Sphaerodoridae, respectively have been included. We chose species described by us when it was possible in order to interpret the characters directly on the material we had studied. That was the case for the species *Chrysopetalum maculata* Aguado, Capa & San Martín, 2003, *Pisione longispinulata* Aguado & San Martín, 2004 and *Sphaerodoropsis anae* Aguado & Rouse, 2006.

The family Nautiliniellidae has been considered as a potential sister group of syllids (Glasby, 1993). However, these animals are quite modified due to their parasitic way of life and hence, they were not included herein.

Table 3. Material examined and consulted references.

Taxa	**Examined material**	**References**
Pisione longispinulata Aguado & San Martín, 2004	Type series MNCN16.01/8876a-b	Aguado & San Martín, 2004
Neanthes virens (Sars, 1835)		Núñez, 2004
Chrysopetalum maculata Aguado, Capa & San Martín, 2003	Type series MNCN16.01/8530a-b	Aguado, Capa & San Martín, 2003
Sphaerodoropsis anae Aguado & Rouse, 2006	Type series MNCN16.01/10817-10818; SAM E3634-35	Aguado & Rouse, 2006
Alcyonosyllis phili Glasby & Watson, 2001	Paratypes 6910-6912NHML; MNCN 16.01/8712 (5)	Glasby & Watson, 2001
Amblyosyllis speciosa Izuka, 1912	KMNH IvR 700,136-138 (4), MNCN 16.01/11004 (1)	Imajima and Hartman, 1964; Imajima, 1966b; Pernet, 1998; Aguado, San Martín & Nishi, submitted
Anguillosyllis capensis Day, 1963	Holotype NHML 1963.1.29	Day, 1963; Day, 1967; Böggemann & Purschke, 2005; Aguado & San Martín, in press
Anoplosyllis edentula Claparède, 1868	MNCN 16.01/183, 6736, 6737	Cognetti-Varriale, 1971; San Martín, 2003
Astreptosyllis acrassiseta Kudenov & Dorsey, 1982	Paratype AM W18587 (1); AM W22995 (1)	Kudenov & Dorsey, 1982; San Martín & Hutchings, 2006

Bollandia antipathicola Glasby, 1994	Holotype USMN 169157; paratypes USMN 169163; USMN 168158; USMN 169162; USMN 169161; USMN 169164; USMN 169160; NHML 3202-3203	Glasby, 1994
Brachysyllis infuscata (Ehlers, 1901)	Holotype ZMB 6742	Ehlers, 1901a; Ehlers, 1901b; Augener, 1922; Imajima & Hartman, 1964; Aguado & San Martín, in press
Branchiosyllis oculata Ehlers, 1887	Syntype NFMN 6745; AM W30112-3; USNM 109269-70	Uebelacker, 1984; San Martín, 1991
Brania pusilla (Dujardin, 1851)	MNCN 16.01/7070- 7075, 16.01/8192- 8244	San Martín, 2003
Brania gallagheri Perkins, 1981	Holotype USNM 60209; Paratypes USNM 54502-4	Perkins, 1981
Cicese sphaerosylliphormis Díaz-Castañeda & San Martín, 2001	Holotype UANL BSQ R8, Paratypes UANL BSQ R17, R23	Díaz-Castañeda & San Martín, 2001
Clavisyllis alternata Knox, 1957	NIWA 4067	Knox, 1957; Aguado & San Martín, in press
Dentatisyllis mortoni Ding, Licher & Westheide, 1998	Holotype SMF 5582; Paratypes SMF 5583; NHML 1292; NHML1293-1301	Ding, Licher & Westheide, 1998
Dioplosyllis cirrosa Gidholm, 1962	Type lost	Gidholm, 1962
Epigamia labordai (San Martín & López, 2002)	MNCN 16.01/6096, 6097, 9218	San Martín & López, 2002; San Martín, 2003; Nygren, 2004
Erinaceusyllis serratosetosa (Hartmann-Schröder, 1982)	MNCN 16.01/XXX	Hartmann-Schröder, 1982; San Martín, 2003
Eurysyllis tuberculata Ehlers, 1864	AM W30132-39; USNM 59104-5; USNM 59101; USNM 59103	San Martín, 2003; San Martín *et al*., in press
Eusyllis blomstrandi Malmgren, 1867	MNCN 16.01/XXX	San Martín, 2003
Exogone naidina Örsted, 1845	MNCN 16.01/7645-7839	San Martín, 2003; Mastrodonato *et al*., 2003
Trypanoseta ohma (Imajima & Hartmann, 1964)	CBM-ZW 996; MNCN/ADN 9577	Imajima & Hartman, 1964; Imajima, 1966 d; Aguado, San Martín & Nishi, submitted
Haplosyllides floridana Augener, 1924	Holotype ZMB 6608; MNCN 16.01/8806, 8808, 8809, 8810	Uebelacker, 1982; San Martín *et al*., 1997
Haplosyllis spongicola (Grube, 1855)	Type MPW 399; MNCN 16.01/2080-2087	San Martín, 2003
Imajimaea zonata (Mohamed, 1973)		Nygren, 2004
Inermosyllis balearica (San Martín, 1982)	Type series MNCN 16.01/199; SMF16361	San Martín, 1982; 2003; Aguado & San Martín, 2007
Karroonsyllis exogoneformis San Martín & López, 2003	Type series AM W26500-1	San Martín & López, 2003
Lamellisyllis comans Day, 1960	Holotype SAM A20924	Day, 1960; 1967; Aguado & San Martín, in press
Levidorum hartmanae Perkins, 1987	MNCN 16.01/XXX	Perkins, 1987; San Martín, 2003; Nygren, 2003
Murrindisyllis kooromundrola San Martín, Aguado & Murray, 2007	Type series AM W.23066, AM W.23062, AM W.29522-27, 29, 31, 33, 35	San Martín *et al*., 2007
Myrianida prolifera (Müller, 1788)	MNCN 16.01/196, 16.01/6468-6489	Gidholm, 1965; San Martín, 2003; Nygren, 2004
Miscellania dentata Martín, Alós & Sardá, 1990	MNCN 16.01/719	Martín *et al*., 1990; San Martín, 2003
Neopetitia amphophthalma (Siewing, 1956)	MNCN 16.01/XXX	Bührmann *et al*., 1996a, 1996b; San Martín, 2003
Nooralia bulgannabouyanga San Martín, 2002	Type series AM W27399, AM W27400-42	San Martín, 2002; 2005
Nuchalosyllis lamellicornis Rullier & Amoreux, 1979	Holotype MNHN 1302	Rullier & Amoreux, 1979 ; Aguado & San Martín, in press
Nudisyllis pulligera (Krohn, 1852)	MNCN 16.01/XXX; MNCN/ADN 9581; ESFM- POL 135-245 (1)	San Martín, 2003
Odontosyllis fulgurans (Audouin & Milne Edwards, 1834)	MNCN 16.01/7570-7605; MNCN/ADN 9582; SMF 16407, 16456, 16373	San Martín, 2003; Aguado & San Martín, 2007
Opisthodonta morena Langerhans, 1879	MNCN 16.01/6689-6691; NMW 2443	San Martín, 2003
Opisthosyllis brunnea Langerhans, 1879	MNCN 16.01/197, 750, 8995, 11025; NMW 674; AM W31399; AM W31402; AM W31398	San Martín, 2003; Aguado *et al*., 2005; San Martín *et al*., submitted b
Pachyprocerastea hydrozoicola (Hartmann-Schröder, 1992)		Hartmann-Schröder, 1992; Nygren, 2004
Palposyllis prosostoma Hartmann-Schröder, 1977	MNCN 16.01/6604; NHML 126-127	Hartmann-Schröder, 1977; San Martín, 2003
Paraehlersia ferrugina (Langerhans, 1881)	Type NMW2302	San Martín, 2003

Parexogone hebes (Webster & Benedict, 1884)	MNCN 16.01/6740-6743	San Martín, 2003
Parahaplosyllis brevicirra Hartmann-Schröder, 1990	Type series ZMH P9959-60 AM W26341, AM W26327, AM W26328	Hartmann-Schröder, 1990
Paraopisthosyllis ornaticirra San Martín & Hutchings, 2006	Holotype AM W28949	San Martín & Hutchings, 2006
Parapionosyllis minuta (Pierantoni, 1903)	MNCN 16.01/6836-6844	Pierantoni, 1903; San Martín, 2003
Paraproceraea tamana (Imajima, 1966)		Imajima, 1966a; Nygren, 2004
Paraprocerastea crocantinae San Martín & Alós, 1989	Type series MNCN 16.01/620, 622	San Martín & Alós, 1989; Nygren, 2004
Parasphaerosyllis indica Monro, 1937	Holotype NHML 156; USMN 52348; USNM 98208-9;	Westheide, 1974
Pionosyllis enigmatica (Wesenberg-Lund, 1950)	Holotype ZMUC-POL-16; ZMH V-977; MNCN/ADN 9586; MNCN	San Martín, 2003; San Martín *et al*., submitted a
Plakosyllis brevipes Hartmann-Schröder, 1956	Holotype ZMH P-14765; MNCN 16.01/6605; AM W26330-31; SMF 9893, 11387	San Martín *et al*., in press
Planicirrata proceraeae (Hartmann-Schröder & Rosendfeld, 1990)		Hartmann-Schröder & Rosendfeld, 1990; Nygren, 2004
Procerastea halleziana Malaquin, 1893	MNCN 16.01/7094-7108	San Martín, 2003; Nygren, 2004
Proceraea picta Ehlers, 1864	MNCN 16.01/XXX; MNCN/ADN 9588	Hamond, 1967; San Martín, 2003; Nygren, 2004
Proshaerosyllis xarifae (Hartmann-Schröder, 1960)	MNCN 16.01/6405-6409, 166, 10916, 10935; MNCN/ADN 9590; AM W26558	San Martín, 2003; 2005
Psammosyllis wui Ding & Westheide, 1997		Ding & Westheide, 1997
Rhopalosyllis hamulifera Augener, 1913	Syntypes HZM V-10076, HZM V-7963; AM W30158; AM W26740	San Martín *et al*., in press
Salvatoria clavata (Claparède, 1863)	MNCN/ADN 9591; MNCN 16.01/10992	San Martín, 2003
Sphaerosyllis hystrix Claparède, 1863	MNCN/ADN 9594; MNCN 16.01/6162-6262	San Martín, 2003
Streptodontha pterochaeta (Southern, 1914)	AM W22989	San Martín & Hutchings, 2006
Streptospinigera heteroseta Kudenov, 1983	Holotype USNM 74489, Paratype USNM 74490	Kudenov, 1983
Streptosyllis websteri Southern, 1914	Syntype NHML 37; MNCN 16.01/209	San Martín, 2003; Aguado & San Martín, 2006
Syllides japonicus Imajima, 1966	MNCN 16.01/XXX	Imajima, 1966b; San Martín, 2003
Syllis prolifera Krohn, 1852	MNCN 16.01/8270- 8380	San Martín, 2003
Trypanosyllis aeolis Langerhans, 1879	MNCN 16.01/6715-6718	San Martín, 2003
Virchowia clavata (langerhans, 1879)	Syntype NMW 2604	San Martín, 2003; Nygren, 2004
Xenosyllis scabra (Ehlers, 1864)	MNCN 16.01/6613- 6640; USNM 74099	San Martín, 2003

MNCN 16.01/XXX: Waiting for catalogue number

Morphological characters and character states

The "C-method" propoused by Pleijel (1995) was used for character scoring. The codification scheme, included absent-preset characters and unordered multistate characters (Table 4). Complex features were analyzed in several characters, the first one referring to the absence/presence of the whole trait, whereas different states of the complex feature were coded as subsidiary characters. Terminals coded as absent for the more general characters were coded as 'inapplicable' for the subsidiary characters. Autapomorphies and invariant characters were excluded. Most of the species of same genus were anatomically uniform for the selected characters. There were, however,

several instances where polymorphisms were apparent within some genera. In all of these cases the condition that is found in the selected terminal of the genus was used to determine the score.

Table 4. Morphological characters and characters states.

1. Colour pattern. 0: absent; 1: present
2. Number of segments. 0: > 100; 1: 50-100; 2: 15-50; 3: <15
3. Length of body. 0: macrofaunal (more than 10 mm); 1: intermediate (between 5 y 10); 2: meiofaunal (less than 5 mm)
4. Shape of body. 0: cylindrical; 1: ribbon-liked
5. Shape of segments. 0: rectangular; 1: trapezoidal
6. Constancy in number of segments. 0: unfixed; 1: fixed
7. Preanal segment without chaetae. 0: absent; 1: present
8. Longitudinal crests on dorsum. 0: absent; 1: present
9. Dorsal papillae. 0: absent; 1: present
10. Dorsal tubercles. 0: absent; 1: present
11. Dorsal ciliary bands. 0: absent; 1: present
12. Eyes. 0: absent; 1: present
13. Number of eyes. 0: two pairs; 1: one pair
14. Ocular spots. 0: absent; 1: present
15. Prostomium. 0: no retractile; 1: retractile
16. Occipital lobe. 0: absent; 1: present
17. Dorsal row of granules on peristomium. 0: absent; 1: present
18. Lateral wings on peristomium. 0: absent; 1: present
19. Antennae. 0: absent; 1: present
20. Shape of antennae. 0: tapering or digitiform; 1: papiliform; 2: fusiform, onion shaped, skittle shaped; 3: truncheon; 4: spherical; 5: ovoidal
21. Position of median antenna. 0: retarded; 1: in the anterior margin of prostomium
22. Length of median antenna. 0: long; 1: short; 2: very short; 3: very long
23. Length of lateral antenna. 0: long; 1: short; 2: very short; 3: very long
24. Articulation of antennae. 0: smooth; 1: distinctly articulated; 2: indistinctly articulated
25. Size of palps. 0: similar to prostomium; 1: reduced or absent; 2: larger than prostomium (considerably); 3: shorter than prostomium
26. Shape of palps. 0: digitiform or rectangular; 1: triangular
27. Insertion of palps. 0: anterior to prostomium; 1: ventrally to prostomium
28. Orientation of palps. 0: straight; 1: ventrally folded
29. Degree in fussion of palps to each other. 0: free; 1: fused basally or nearly to the middle; 2: totally or practically fused
30. Palps fused to prostomium. 0: absent; 1: present
31. Nuchal organs. 0: absent; 1: present
32. Nuchal epaulettes. 0: absent; 1: present
33. Number of “tentacular” cirri. 0: one pair; 1: two pairs
34. Articulation of “tentacular” cirri. 0: smooth; 1: distinctly articulated; 2: indistinctly articulated
35. Length of dorsal “tentacular” cirri. 0: long; 1: short; 2: very short; 3: very long
36. Notopodia. 0: birrameus; 1: unirrameus
37. Notoacicula. 0. absent, 1. present
38. Parapodial lobes developed. 0: absent; 1: present
39. Parapodial gland opened by pores. 0: absent; 1: present
40. Ventral cirri. 0: present; 1: absent
41. Ventral cirri inflated. 0: absent; 1: present
42. Ventral cirri insertion. 0: proximal; 1: medial; 2: distal
43. Pores on anterior ventral cirri. 0: absent; 1: present
44. Posterior ventral cirri elongated. 0: absent; 1: present
45. Dorsal cirri. 0: Present in all (or practically all) segments; 1: Absent in all (or practically all) segments
46. Shape of dorsal cirri. 0: tapering or digitiform; 1: papiliform; 2: fusiform, onion shape, skittle; 3: truncheon; 4: ovoidal; 5: spherical
47. Dorsal cirri inflated. 0: absent; 1: present
48. Dorsal cirri in spiral over dorsum. 0: absent; 1: present
49. Articulation of anterior dorsal cirri. 0: smooth; 1: distinctly articulated; 2: indistinctly articulated
50. Articulation of midbody and posterior dorsal cirri. 0: smooth; 1: distinctly articulated; 2: indistinctly articulated
51. Articulation of posterior dorsal cirri. 0: smooth; 1: distinctly articulated; 2: indistinctly articulated
52. Dorsal cirri showing a fixed articulation pattern. 0: absent; 1: present
53. Length of anterior dorsal cirri. 0: long; 1: short; 2: very short; 3: very long
54. Length of midbody dorsal cirri. 0: long; 1: short; 2: very short; 3: very long
55. Length of posterior dorsal cirri. 0: long; 1: short; 2: very short; 3: very long
56. Alternation in length of dorsal cirri. 0: no alternating; 1: alternating
57. Insertion of dorsal cirri. 0: at same level; 1: at different levels (alternating)
58. cirrophore. 0: absent; 1: present
59. Length of anal cirri. 0: long; 1: short

60. Shape of anal cirri. 0: tapering or digitiform; 1: papiliform; 2: fusiform, onion shape, skittle; 3: truncheon; 4: ovoidal; 5: spherical
61. Articulation of anal cirri. 0: smooth; 1: distinctly articulated; 2: indistinctly articulated
62. Anterior aciculae enlarged. 0: absent; 1: present
63. Shape of aciculae. 0: straight; 1: acuminate, tricuspid, lanceolate; 2: rounded or distally expanded
64. Aciculae distally hollow. 0: absent; 1: present
65. Dorsal simple chaetae. 0: absent; 1: present
66. Dorsal simple chaetae. 0: from the beginning; 1: only on posterior segemnts
67. Spines on dorsal simple chaetae. 0: absent; 1: present
68. Shape of dorsal simple chaetae. 0: bidentate; 1: unidentate; 2: bayonet
69. Anterior dorsal simple chaetae modified. 0: absent; 1: present
70. Ventral simple chaetae. 0: absent; 1: present
71. Spines on ventral simple chaetae. 0: absent; 1: present
72. Shape of ventral simple chaetae. 0: bidentate; 1: unidentate
73. Compound chaetae. 0: present; 1: absent
74. Simple chaetae. 0: absent; 1: present
75. Anterior neurochaetae distinctly different. 0: absent; 1: present
76. Size of falcigers. 0: all similar; 1: anterior ones long, posterior short
77. Length of articles in same fascicle. 0: all similar; 1: differences in length
78. Pseudospiniger-like chaetae. 0: absent; 1: present
79. Anterior falciger chaetae unidentate. 0: absent; 1: present
80. Anterior falciger chaetae bidentate. 0: absent; 1: present
81. Anterior falciger bidentate. 0: bidentate with similar teeth; 1: bidentate with distal tooth larger than proximal one; 2: bidentate with proximal tooth larger than distal one
82. Posterior falcigers unidentate. 0: absent; 1: present
83. Posterior falcigers bidentate. 0: absent; 1: present
84. Posterior falcigers bidentate. 0: teeth similar is size; 1: distal tooth larger than proximal one; 2: proximal tooth larger than distal one
85. Unidentate falcigers with rounded tip. 0: absent; 1: present
86. Bidentate neurochaetae in two levels. 0: absent; 1: present
87. Chaetal spinulation. 0: absent; 1: present
88. Shafts chambered. 0: present; 1: absent
89. Proventricle. 0: absent; 1: present
90. Shape of proventricle. 0: cuadrangular or rectangular; 1: barrel shaped
91. Length of proventricle. 0: short; 1: long; 2: very long
92. Chitinous inner proboscis lining. 0: absent; 1: present
93. Length of pharynx. 0: similar or longer to proventricle; 1: shorter than proventricle
94. Shape of pharynx. 0: straight; 1: sinuous
95. Width of pharynx. 0: narrow; 1: broad; 2: very narrow
96. Jaws. 0: absent; 1: present
97. Pharyngeal tooth. 0: absent; 1: present
98. Position of pharyngeal tooth. 0: anterior or retarded; 1: middle to posterior
99. Pharyngeal tooth shape. 0: conical; 1: rhomboidal
100. Trepan. 0: absent; 1: present
101. Ventral denticle arc. 0: absent; 1: present
102. Modifications for reproduction. 0: absent; 1: present
103. Reproductive mode. 0: epigamy; 1: eschizogamy
104. Stolons with distinct regions. 0: with distinct regions; 1: without distinct regions
105. Dimorphism in stolons. 0: present; 1: absent
106. Scissiparity. 0: anterior scissiparity; 1: posterior scissiparity
107. Development of stolon. 0: dorsal; 1: ventral
108. Brooding. 0: absent; 1: present
109. Kind of brooding. 0: by notochaetae; 1: by nephridial pore; 2: in gelatinous masses; 3: in sacks; 4: viviparity
110. Postembrionic development. 0: planctonic larval development; 1: direct development
111. Change in articulation of dorsal cirri from juveniles to adults. 0: absent; 1: present

Description of characters used in the analysis

Characters and states are summarized in Table 4. Numbers in parentheses correspond to the characters. The matrix is shown in the *Anexus* section.

Body (1-7). The colour pattern (Fig. 1) is a feature difficult to distinguish in preserved material; however, it has been included herein because it is well known for most of the selected species studied herein. The categories of macrofaunal (more than 10 mm), intermediate (between 5 and 10 mm) and meiofaunal (less than 5 mm) are based on Mare (1942). The number of segments and body length are coded as two different characters since it is possible to find macrofaunal genera (long animals) with a reduced number of segments (e. g. *Amblyosyllis* Grube, 1857 and *Brachysyllis* Imajima & Hartman, 1964) (Figs. 1G, H). The outgroup and most of syllids present a body circular in section with a flattened ventrum (Fig. 2A); however, some genera (e. g. *Trypanosyllis*, *Eurysyllis* Ehlers, 1864, *Plakosyllis* Hartmann-Schröder, 1956 and *Nuchalosyllis* Rullier & Amoureux, 1979) show a distinct ribbon-shaped body, quite wide and narrow in section (Figs. 3B-D). Segments are often rectangular in shape with the exception of those of *Amblyosyllis* and *Brachysyllis*, which are trapezoidal (Figs. 1G, H). These latter genera also present a constant number of segments during their life (between 10 and 20, depending on the species), and a preanal segment without chaetae.

Ornamentation (8-11). We have considered as ornamentation several traits that are usually located on the dorsum of some syllids. The presence of longitudinal crests over the dorsum is not taken into account in most of the species' descriptions of *Trypanosyllis*, *Rhopalosyllis* Augener, 1913 and *Xenosyllis* Marion & Bobretzky, 1875. However, after detailed studies using SEM they seem to be quite common in these genera (San Martín *et al.*, in press) (Fig. 2C). Papillae are often found in Exogoninae and also in some Eusyllinae and Syllinae genera (Figs. 2G, H; 4C, E, F), while tubercles are only present in the genus *Eurysyllis* (Fig. 2D). However since they are also common in Sphaerodoridae, and present in the outgroup *S. anae*, we decided to include the character even though it is not demonstrated that both features are the same structure. Dorsal ciliary bands are difficult to see using optic microscopy, but have been found in several species studied under SEM (Figs. 2E, F; 3A). We think that probably more taxa of Syllidae have this feature, however, we only included the information available and when there were doubts about its presence we coded it as unknown (?).

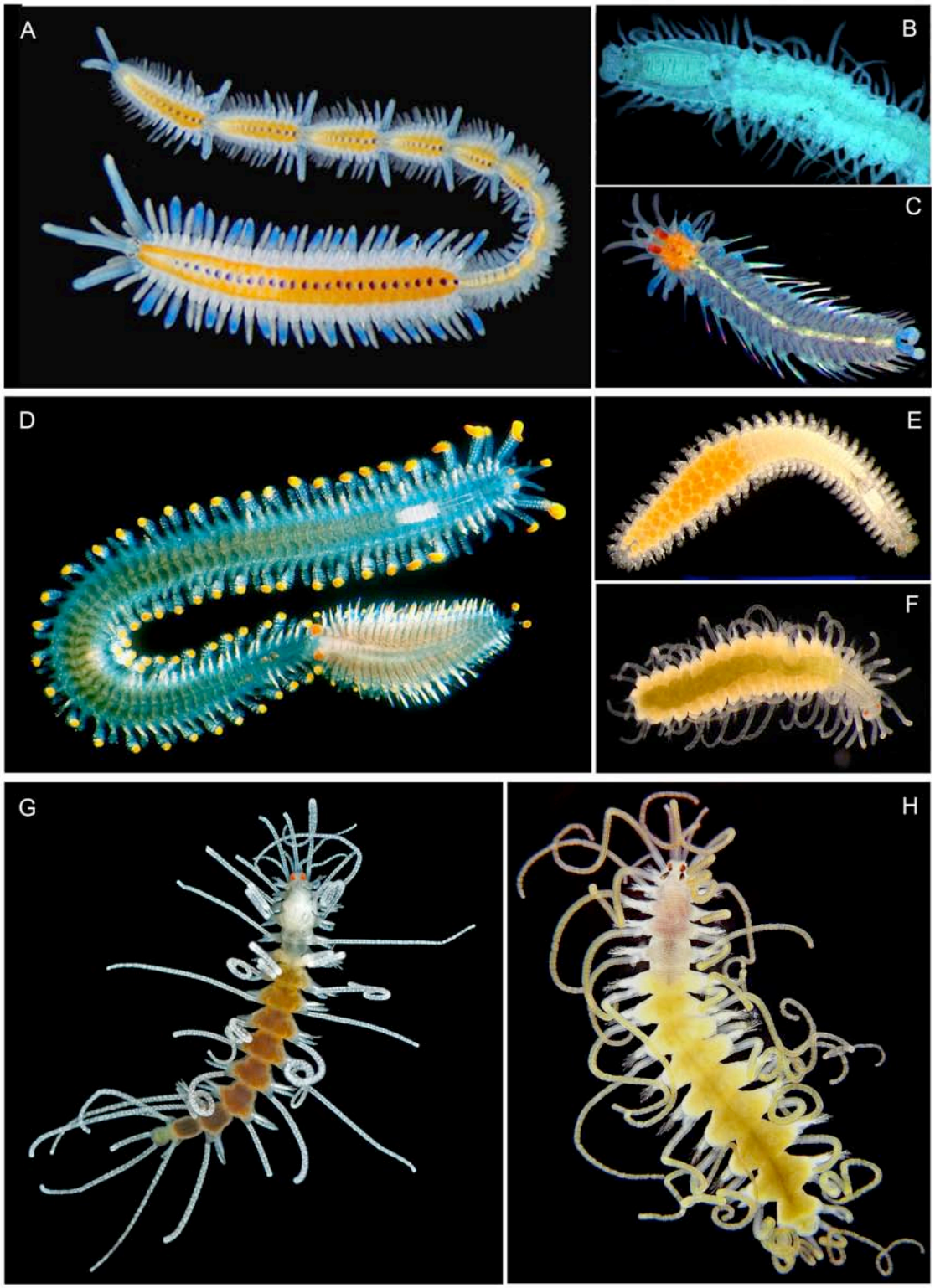

Figure 1. *Myrianida pachycera*, picture by G. Rouse; B. *Salvatoria* sp., picture by R. Gallego; C. Male stolon of *Myrianida pachycera*, picture by M. Capa; D. *Trypanosyllis* sp., picture by G. Rouse; E. *Eurysyllis* sp., picture by G. Rouse; F. *Syllides* sp., picture by G. Rouse; G. *Amblyosyllis* sp., picture by A. Nygren; H. *Amblyosyllis* sp., picture by G. Rouse.

Prostomium and peristomium (12-18). Eyes are usually present in both outgroup and ingroup, excepting *Sphaerodoropsis* Hartman & Fauchald, 1971, *Anguillosyllis* Day, 1963 and *Palposyllis* Hartmann-Schröder, 1977. These taxa live at deep bottoms and the absence of eyes could be a secondary lost; probably it is an adaptation to their habitat. The number of eyes is quite constant in syllids, having most of them two pairs; few genera present only a single pair (*Haplosyllides* Augener, 1924, *Murrindisyllis* San Martín, Aguado & Murray, 2007 and *Neopetitia* San Martín, 2003). The common condition between outgroups is having two pairs of eyes, excepting *Pisione* Grube, 1856 which has only one. One character about ocular spots has been also included although it is a feature difficult to observe in the preserved material, as previous authors have argued (Nygren, 1999). However its presence/absence is well known for most of the species selected herein. In some genera of Exogoninae, the prostomium is retractile and can be partially covered by the peristomium (Fig. 2H). The presence of an occipital lobe (Figs. 2E; 3A) arising from peristomium and partially covering the prostomium is present in some species of *Odontosyllis* Claparède, 1863 and *Opisthosyllis* Langerhans, 1879. However this character is not constant in both genera. It is present in the selected terminals *O. fulgurans* (Audouin & Milne Edwards, 1834) and *O. brunnea* Langerhans, 1879. *Streptosyllis, Syllides* and *Anoplosyllis* Claparède, 1868 usually have a row of granules on the peristomium (San Martín & Hutchings, 2006) (Fig. 6A). This feature is absent in the rest of the syllid genera. Two lateral projections or lateral wings have been described for some species of *Erinaceusyllis* San Martín, 2005 and *Cicese* Díaz-Castañeda & San Martín, 2001 (Fig. 3B).

Antennae (19-24). Length and insertion of antennae are quite variable within Syllidae. In contrast, the articulation pattern seems to be constant in the subfamilies (articulated antennae for Syllinae (Figs. 2C, 4A), not articulated for Autolytinae (Figs. 1A, C) and Exogoninae (Figs. 3B, C, 4C), and smooth or indistinctly articulated for Eusyllinae (Figs. 1G, H, 3A, F, 4B). The articulation and shape of antennae usually coincides with dorsal and tentacular cirri. Nevertheless, it is quite remarkable that they are smooth for *Syllides, Streptosyllis, Streptospinigera* Kudenov, 1983 and *Astreptosyllis* although their midbody and posterior dorsal cirri are mostly articulated. We have considered that the antennae are long when they are longer than the prostomium plus the palps; short when

they are shorter; very short when they are very reduced or papilliform; and very long when they are reaching at least to the eighth segment.

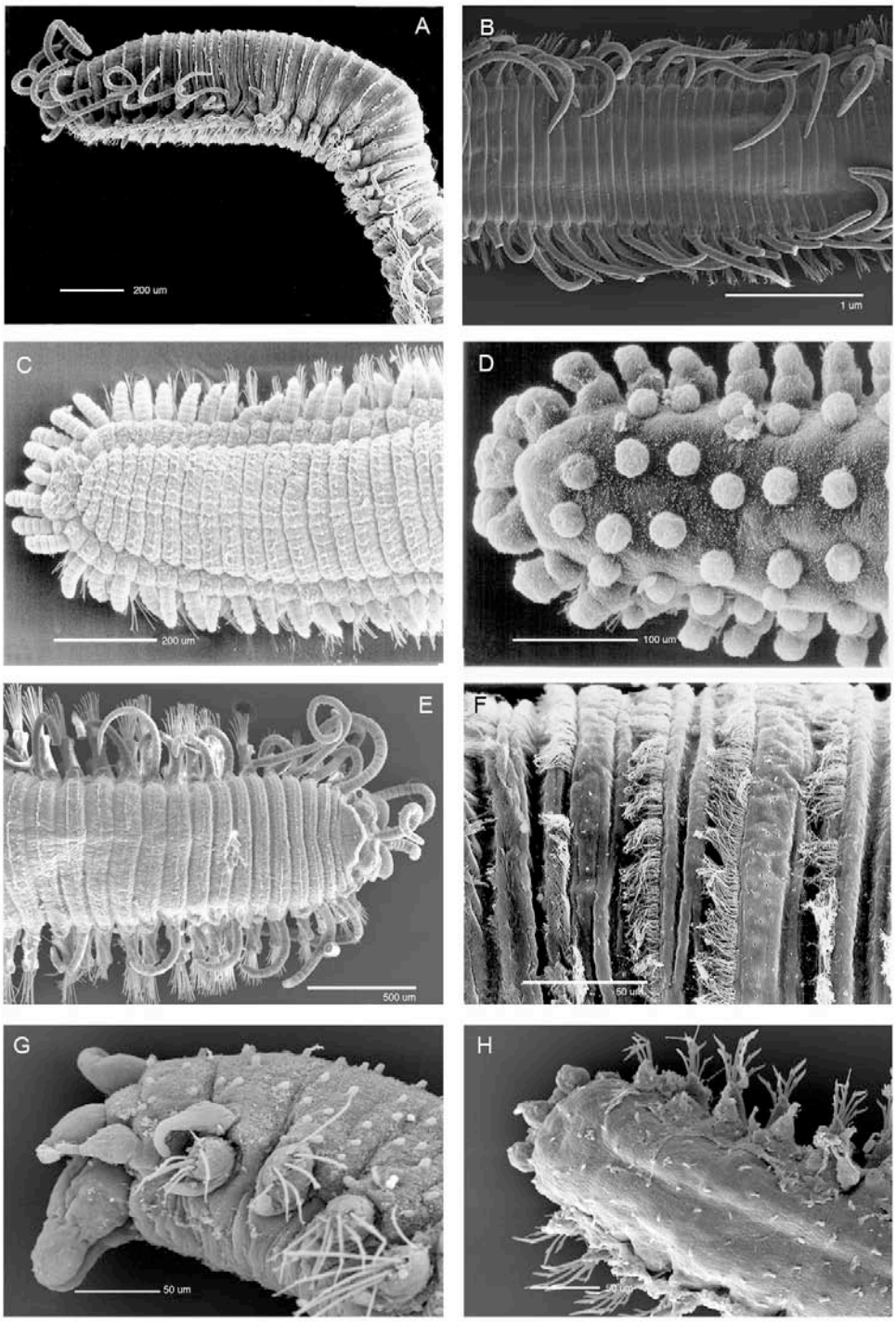

Figure 2. SEM. A. *Paraehlersia ferrugina*, lateral view (San Martín, 2003); B. *Trypanosyllis zebra*, midbody segments, dorsal view (San Martín *et al.*, in press); C. *Xenosyllis scabra*, anterior end, dorsal view (San Martín, 2003); D. *Eurysyllis tuberculata*, anterior end, dorsal view (San Martín, 2003); E. *Odontosyllis undecimdonta*, anterior end, dorsal view (Aguado *et al.*, submitted); F. *Paraehlersia ferrugina*, midbody segments, lateral view (San Martín, 2003); G. *Sphaerosyllis hirsuta*, anterior end, lateral view (San Martín, 2005); H. *Sphaerosyllis capensis*, anterior end, dorsal view (San Martín, 2005).

Palps (25-30). The palps are clearly conical (subtriangular from dorsal view) in syllids, while terminals in the outgroup have other shapes (e. g. digitiform in *Pisione*, bipartite in Nereididae, cylindrical in Chrysopetalidae). The ventral pair of "antennae" (Borowski, 1994) in *Sphaerodoropsis* has been considered as palps (Rouse & Fauchald, 1997; Pleijel & Dahlgren, 1998; Pleijel, 2001c; Worsaae *et al.*, 2005; Aguado & Rouse, 2006). The degree of fusion between the pair of palps has been one of the main characters used to differentiate subfamilies (see Table 1); however, a detailed examination of members of Eusyllinae and Syllinae demonstrated that this feature

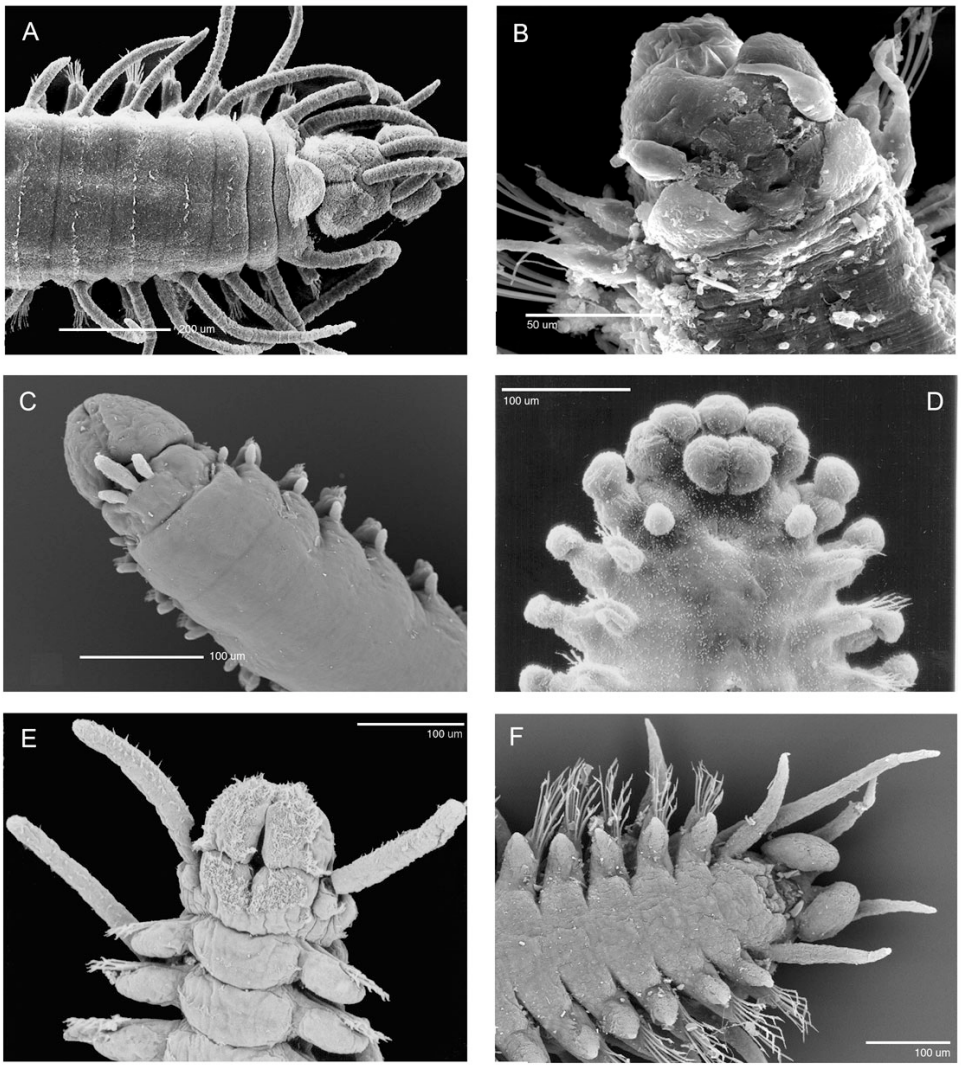

Figure 3. SEM. A. *Odontosyllis fulgurans,* anterior end, dorsal view (San Martín, 2003); B. *Erynaceusyllis kathrynae*, anterior end, dorsal view (San Martín, 2005); C. *Exogone goorapuranga*, anterior end, dorsal view (San Martín, 2005); D. *Eurysyllis tuberculata*, anterior end, ventral view (San Martín, 2003); E. *Myrianida prolifera*, anterior end, ventral view (San Martín, 2003); F. *Eusyllis kupffferi*, anterior end, ventral view (San Martín & Hutchigs, 2006).

shows a high degree of plasticity. There are numerous examples of Syllinae and Eusyllinae genera with basally fused palps, and they can be medially or completely fused in Autolytinae and Exogoninae (Figs. 3B, C). Some genera of Autolytinae have very reduced palps (Fig. 3E), being practically absent in several taxa (Fig. 4D) (San Martín, 2003; Nygren, 2004). In the rest of Syllidae, they are inserted on the anterior margin of prostomium, which is the usual condition (Fig. 4A), or occasionally inserted ventrally to prostomium (in *Eurysyllis*, *Plakosyllis* and *Xenosyllis*) (Fig. 3D). In these latter genera, palps are commonly reduced. In *Murrindisyllis* and *Palposyllis* there is no insertion groove showing the limit between palps and prostomium, being both structures completely fused.

Nuchal organs (31-32). Nuchal organs have been considered a synapomorphy of Polychaetes (Rouse & Fauchald, 1997; Rouse & Pleijel, 2001). They are usually ciliated grooves or pits (Fig. 5A), sometimes eversible as caruncula (Chrysopetalidae or Amphinomida), as a posterior elongation of the head (in some Spionidae), or as nuchal lappets (several genera of Syllidae) (Figs. 5B-D). However, nuchal organs are absent in some few polychaete groups (presumably losses *fide* Rouse & Pleijel, 2001), between them *Pisione* and *Sphaerodoropsis*. Typically, nuchal organs of syllids are two ciliated grooves between prostomium and peristomium (Fig. 5A), but Autolytinae shows external nuchal organs as nuchal lappets instead of grooves (Fig. 5C). Although it has been considered as a diagnostic character of Autolytinae (see Table 1), some other genera of Eusyllinae, such as *Amblyosyllis*, *Clavisyllis* Knox, 1957 and *Lamellisyllis* Day, 1960 also have nuchal lappets (Figs. 5B, D). In addition, *Nuchalosyllis*, an enigmatic genus of Syllinae, possess nuchal lappets divided in several transversal lamellae.

"Tentacular" cirri (33-35). Dorsal or ventral cirri of cephalized segment(s), which usually differ in length from the remainder cirri, are commonly called tentacular cirri (Rouse & Pleijel, 2001). However, their origin is considered misleading since they might not be peristomial structures (Pleijel & Dahlgren, 1998). Rouse & Pleijel (2001) considered them segmental structures and suggested that, in absence of conclusive evidence, they might be considered as pertaining to the first segment. However, the term "tentacular" is used herein since it is part of the general and commonly used terminology of Syllidae appendages. In Syllidae, the first segment lacks chaetae and

typically presents two pairs of "tentacular" cirri (Figs. 3A, F, 4A, B, E), although there are numerous exceptions with only one pair (*Anguillosyllis*, *Erinaceusyllis*, *Karroonsyllis* San Martín & López, 2003, *Parexogone* Mesnil & Caullery, 1918, *Parapionosyllis* Fauvel, 1923, *Prosphaerosyllis* San Martín, 1984 and *Sphaerosyllis* Claparède, 1863) (Figs. 2G, 3C, 4C). *Levidorum* Hartman, 1967 lacks "tentacular" cirri, as well as antennae and dorsal and ventral cirri (Fig. 4D).

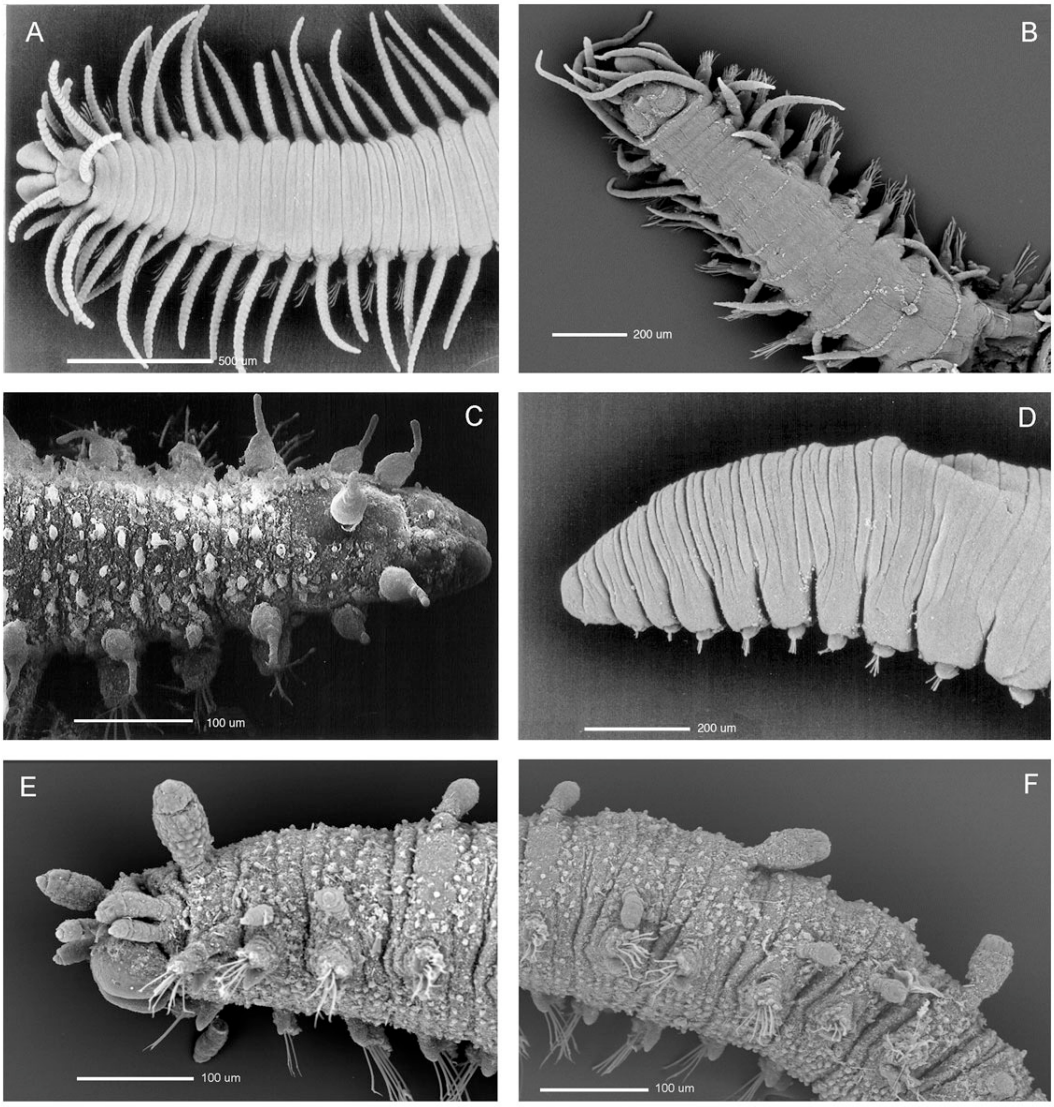

Figure 4. SEM. A. *Syllis amica*, anterior end, dorsal view (San Martín, 2003); B. *Eusyllis kupfferi*, anterior end, dorsal view (San Martín & Hutchings, 2006); C. *Sphaerosyllis pirifera*, anterior end, dorsal view (San Martín, 2003); D. *Levidorum pori*, anterior end, lateral view (San Martín, 2003); E. *Paraopisthosyllis alternocirra*, anterior end, lateral view (San Martín & Hutchings, 2006); F. *Paraopisthosyllis alternocirra*, midbody segments, lateral view (San Martín & Hutchings, 2006).

In the outgroup, *Sphaerodoropsis* has only one pair of "tentacular" cirri, the rest of terminals present two pairs, excepting *Neanthes* Kinberg, 1865 which has more than two. The shape of "tentacular" cirri is usually the same as dorsal cirri and it has not been included as a different character. For coding the length of "tentacular" cirri we have considered same criteria used for dorsal cirri (see below).

Parapodia (36-39). The parapodia of Syllidae, Pisionidae and Sphaerodoridae are unirramous (Figs. 5E, F), while they are birramous in Nereididae and Chrysopetalidae. However, Pisionidae maintains the notoacicula, while it is absent in Syllidae and Sphaerodoridae. Several taxa present moderately long expansions distally on neuropodia, which are called parapodial lobes. They can be pre-chaetal or post-chaetal depending on their position. We have not considered this distinction in the characters because in some taxa, the position is confusing being also possible to consider them as above-chaetae and/or behind-chaetae lobes. Some genera of Exogoninae (*Parapionosyllis*, *Sphaerosyllis* and *Brania* Quatrefages, 1866) have parapodial glands, which are opened on each segment by pores (San Martín, 2003; San Martín & Hutchings, 2006) (Fig. 5G).

Ventral cirri (40-44). In Autolytinae, ventral cirri are considered reduced and fused to the parapodial lobes (Nygren, 1999, 2004; San Martín, 2003) (Figs. 3E, 6B); however, a detailed study of the ontogeny of this group might be necessary to definitively assess this supposition. Partial fusion of ventral cirri to parapodia is also common in some species of *Opisthodonta* Langerhans, 1879 (San Martín & Hutchings, 2006), a Eusyllinae member, althought these taxa have not been considered as terminals herein. Ventral cirri are commonly digitiform in shape (Fig. 5E), but they can be inflated in *Nooralia* San Martín, 2002, and polymorphic in *Odontosyllis* and *Pionosyllis* (coded as inflated for *O. fulgurans* and *P. enigmatica* (Wesenberg-Lund, 1950)). The ventral cirri are commonly proximally inserted in the parapodia but some taxa have cirri medially inserted (*Astreptosyllis*, *Streptospinigera*, *Streptosyllis*, *Syllides* and *Anoplosyllis*) (Fig, 6D), or distally inserted (*Dioplosyllis* Gidholm, 1962, *Neopetitia* and *Anguillosyllis*) (San Martín, 2003; Aguado & San Martín, in press). Posterior ventral cirri are longer than those on anterior segments in *Astreptosyllis*, *Streptospinigera* and *Streptosyllis*. The presence of pores on ventral cirri has been proved for *Eurysyllis*, *Plakosyllis* and

Xenosyllis after SEM studies (San Martín, 2003; San Martín *et al.*, in press) (Fig. 5H). They might be also present in other genera.

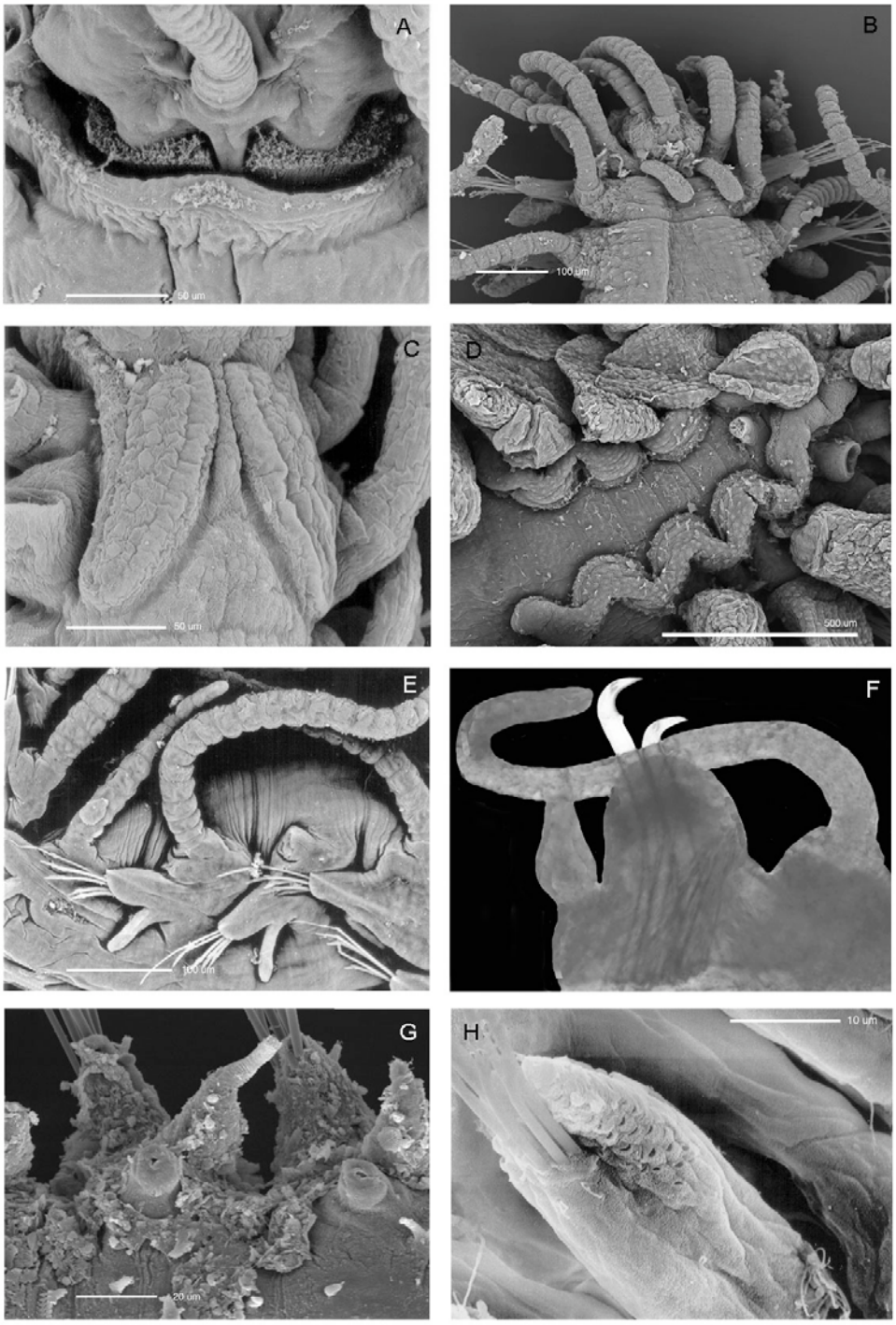

Figure 5. SEM. A. *Syllis corallicola*, nuchal organs (San Martín, 2003); B. *Amblyosyllis enigmatica*, anterior end, dorsal view (San Martín & Hutchings, 2006); C. *Proceraea aurantiaca*, nuchal epaulettes (San Martín, 2003); D. *Clavisyllis alternata*, nuchal epaulettes (Aguado & San Martín, in press); E. *Syllis beneliahuae*, parapodia, lateral view (San Martín, 2003); F. *Alcyonosylllis* sp., parapodium, lateral view (photo by C. Glasby); G. *Sphaerosyllis densopapillata*, gland pores on parapodia, ventral view (San Martín, 2005); H. *Plakosyllis brevipes*, gland pores on anterior ventral cirri (San Martín, 2003).

Dosal cirri (45-59). Lateral macrotubercles in *Sphaerodoropsis anae* were initially considered as dorsal cirri (Ruderman, 1911; Reimers, 1933) but they are currently described as different structures called macrotubercles (Fauchald, 1974; Borowski, 1994; Aguado & Rouse, 2006). We show herein the codification according to the current terminology for *Sphaerodoropsis* (absence of dorsal cirri and presence of macrotubercles) (Fauchald, 1974; Borowski, 1994; Aguado & Rouse, 2006). Dorsal cirri are totally absent in *Levidorum* and *Procerastea* Langerhans, 1884 (Fig. 4D). They are wide and expanded in *Clavisyllis* and *Lamellisyllis* and very long, forming spirals over dorsum in *Amblyosyllis*, *Anguillosyllis*, *Dioplosyllis*, *Murrindisyllis* and *Brachysyllis* (Figs. 1G, H). However, the typical condition is having dorsal cirri digitiform in shape and usually alternating in length along the body (Figs. 1D, 4A, 5E). Shape of dorsal cirri is different in Exogoninae, where most of genera have fusiform, papilliform or onion-shaped dorsal cirri (Figs. 2G, H, 3C, 4C). Most of syllids present a strong alternation in length of midbody and posterior cirri. In some species with short dorsal cirri the alternation in length is not very evident (e. g. *Branchiosyllis oculata* Ehlers, 1887, *Haplosyllis spongicola* (Grube, 1855), *Xenosyllis scabra* (Ehlers, 1864)), although they are likely to show it after a detailed examination.

The articulation of dorsal cirri is considered for anterior, midbody and posterior dorsal cirri. The appendages are typically not articulated in Eusyllinae (Figs. 3F, 4B), Exogoninae (Figs. 1B, 2G, 3C, 4C) and Autolytinae (Figs. 1A, 3E), but there are exceptions. In *Amblyosyllis*, usually considered a member of Eusyllinae, some species show indistinctly articulated or pseudoarticulated appendages (Fig. 1G, 5B) (e. g. *A. speciosa* Izuka, 1912). Two genera of Syllinae, *Alcyonosyllis* Glasby & Watson, 2001 and *Haplosyllides* have smooth appendages (Fig. 5F). *Syllides*, *Astreptosyllis*, *Streptospinigera* and many species of *Streptosyllis* have dorsal cirri smooth until the third or fifth dorsal cirri (Fig. 6A). We had coded this special pattern of articulation as an additional character. The selected terminal *Streptosyllis websteri* Southern, 1914 has all dorsal cirri not articulated, although other species of this genus show the same articulation pattern as *Syllides*, *Streptospinigera* and *Astreptosyllis*. The reverse situation occurs in some species of Eusyllinae (e. g. *Paraehlersia* San Martín, 2003 and *Eusyllis* Malmgren, 1867) with articulated anterior dorsal cirri, while they are not articulated in the midbody and posterior regions.

The same regions considered to code the articulation of dorsal cirri have been considered to code the length. We have considered that dorsal cirri are long when they are markedly longer than the double length of parapodia (Figs. 3A, 4A); short, when they are approximately the same length or shorter than the double length of parapodia (Fig. 2G); very long when they are considerably longer that several segments (Figs. 1G, H); and very short when they are papilliform or very reduced (Fig. 3C). In *Murrindisyllis*, anterior and posterior dorsal cirri are considerably shorter than those of the midbody region. For coding the length of anterior dorsal cirri, we did not take into account the first dorsal cirri, which is often considerably longer than the remainders. It is usually more similar in length to dorsal "tentacular" cirri. Dorsal cirri of Syllinae are typically long (Fig. 4A), but two genera, *Eurysyllis* and *Plakosyllis*, have them very short and reduced to a single article (Fig. 2D). In *Parasphaerosyllis* Monro, 1937, the dorsal cirri are in two different shapes and lengths: long digitiform dorsal cirri and short elliptical dorsal cirri. We have coded them as long considering that the appearance of elliptical dorsal cirri might be a secondary acquisition and an autapomorphy of this genus. Other terminals, such as *Alcyonosyllis philli* Glasby & Watson, 2001, *Dentatisyllis mortoni* Ding, Licher & Westheide, 1998 and *Odontosyllis gibba* Claparède, 1863, show a clear alternation in length of dorsal cirri, being difficult to define their length. However, these species have been coded as having long dorsal cirri because their cirri are never shorter than the double length of parapodia. The species *Salvatoria clavata* (Claparède, 1863) has been coded as having short dorsal cirri, although some examined specimens had longer dorsal cirri than usual.

In some taxa, dorsal cirri also alternate in their insertion on the parapodia (Figs. 4E, F). This alternation is distinct in *Nuchalosyllis*, *Paraopisthosyllis* Hartmann-Schröder, 1991, *Lamellisyllis, Clavisyllis, Alcyonosyllis*, and also in some species not included herein, such us *Syllis corruscans* Haswell, 1886 and *S. rubicunda* Aguado, San Martín & Nishi, submitted.

Finally, the presence of cirrophore has also been considered. It is a difficult character to visualize in preserved material; however, we could obtain information of most of the species included herein based on our personal observations and previous phylogenetic studies (Nygren, 1999; 2004).

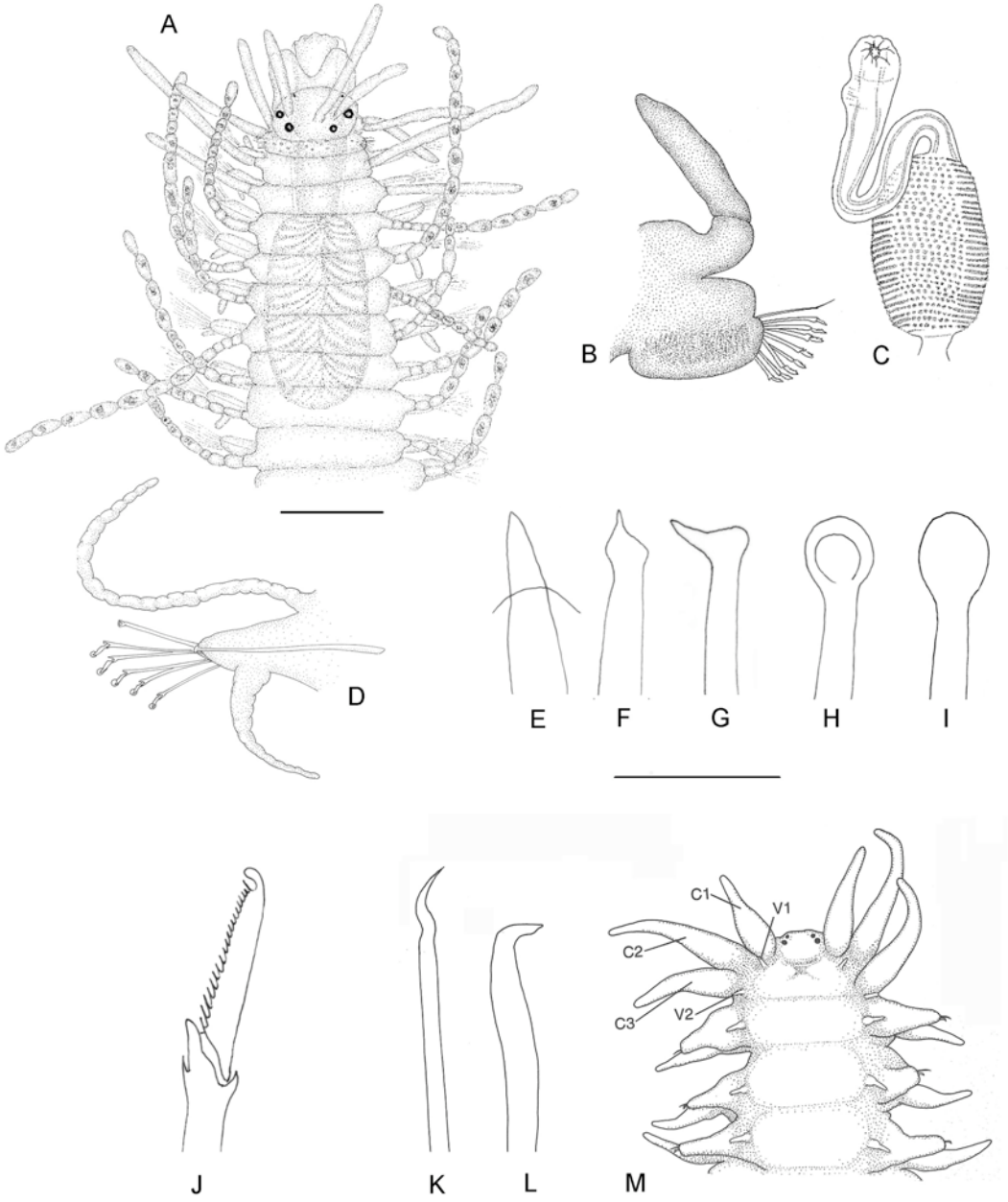

Figure 6. *Syllides tam*, anterior end, dorsal view (San Martín & Hutchings, 2006); B. *Epigamia labordai*, midbody parapodium, lateral view (San Martín, 2003); C. *Epigamia labordai*, pharynx and proventricle (San Martín, 2003); D. *Streptosyllis arenae*, midbody parapodium, lateral view (Aguado & San Martín, in prep.); E. *Prosphaerosyllis multipapillata*, posterior acicula (San Martín, 2005); F. *Prosphaerosyllis isabellae*, midbody acicula (San Martín, 2005); G. *Sphaerosyllis rotundipapillata*, midbody acicula (San Martín, 2005); H. *Brania furcelligera*, midbody acicula (San Martín, 2005); I. *Parexogone tasmanica*, midbody acicula (San Martín, 2005); J. *Brania pusilla*, midbody compound chaeta (San Martín, 2005); K. *Bollandia anthipathicola*, most dorsal chaeta (after Glasby, 1994); L. *Bollandia anthipathicola*, ventral chaeta (after Glasby, 1994); M. *Bollandia anthipathicola*, anterior end, ventral view, C1-C3: "tentacular cirri", V1, V2: ventral cirri (after Glasby, 1994).

Anal appendages (59-61). We have considered that anal cirri are long when they are longer than the pygidium plus the last segment. They coincide in shape with dorsal cirri, but there are several exceptions, such as *Xenosyllis* and *Parexogone brunnea* (Hartman, 1961) (the latter not included herein). Articulation of anal cirri often concurs with dorsal cirri too, but there are several interesting exceptions: they are smooth while posterior dorsal cirri are articulated in *Astreptosyllis*, *Syllides* and *Streptospinigera*; and they are conical and indistinctly articulated in *Xenosyllis* while its dorsal cirri are clearly articulated.

Aciculae (62-64). Genera *Streptodonta*, *Streptospinigera* and *Streptosyllis* present considerably enlarged aciculae on anterior segments (Fig. 7C), becoming abruptly smaller and thinner in midbody and posterior segments. The shape of aciculae is commonly straight and pointed (Fig. 6E), although it can be quite variable, specially in Exogoninae. For instance, they are acuminate (Fig. 6F) in *Erinaceusyllis*, *Salvatoria* McIntosh, 1885 and *Prosphaerosyllis*; and distally expanded and rounded (Figs. 6H, I) in *Brania*, *Exogone* Örsted, 1845 and some *Parexogone* species. The aciculae in *Sphaerosyllis* are different to those of any other of the genera of Syllidae, being distally expanded and bent in a straight angle (Fig. 6G). It has been coded for the terminal *S. hystrix* Claparède, 1863 as distally expanded. The aciculae can be distally hollow as those of *Brania* (Fig. 6H) and *Parapionosyllis* and some species of *Syllis*, *Opisthosyllis* and *Karroonsyllis*.

Dorsal and ventral capillary simple chaetae (65-72). Most of the genera in Syllidae present simple chaetae (Figs. 8A-F) located in the dorsalmost and/or the ventralmost position of the fascicles, called dorsal simple chaetae or ventral simple chaetae, respectively. They are often thinner than the rest of chaetae (capillary in Syllinae and Eusyllinae) (Fig. 8A); or with a markedly different shape (e. g. bayonet shaped chaetae in Autolytinae) (Fig. 7E). They are absent in the outgroup excepting *Pisione*, which has a simple chaetae dorsally located in the chaetal fascicles. The dorsal simple chaetae appear from anterior segments towards the end of the body in Exogoninae, Autolytinae; *Streptosyllis*, *Syllides*, *Astreptosyllis* and *Streptospinigera*; whereas they can only be observed, when present, in the posterior segments of Syllinae and Eusyllinae. Anterior dorsal simple chaetae of *Streptosyllis*, *Astreptosyllis* and

Streptospinigera (Figs. 7A, B) are often bigger and different in shape to those on posterior segments.

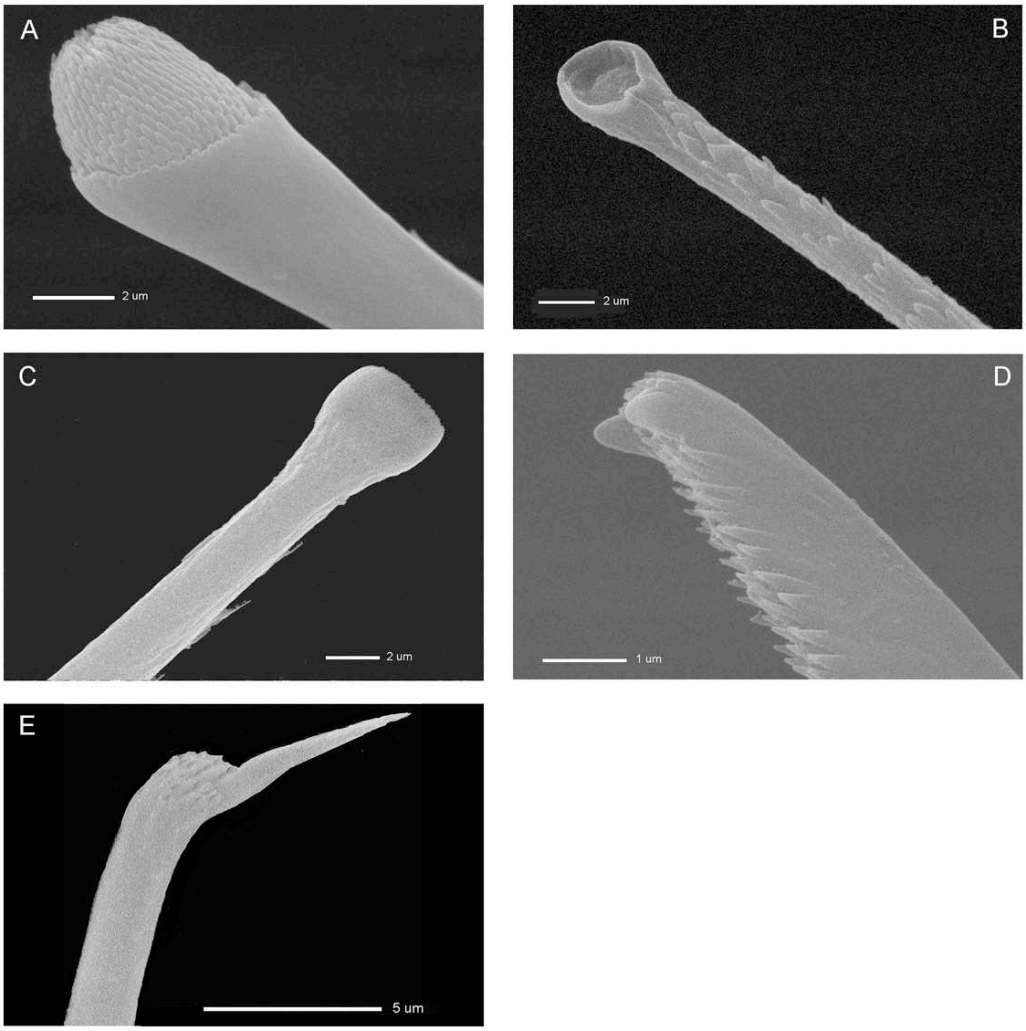

Figure 7. SEM. A. *Astreptosyllis acrassiseta*, detail of distal end of dorsal simple chaeta, midbody parapodium (San Martín & Hutchings, 2006); B. *Streptosyllis aequiseta*, dorsal simple chaeta, posterior parapodium (San Martín & Hutchings, 2006); C. *Streptosyllis aequiseta*, anterior acicula AMW28370 (unpublished picture); D. *Astreptosyllis acrassiseta*, detail of tip of midbody compound chaeta (San Martín & Hutchings, 2006); E. *Proceraea aurantiaca*, bayonet-shaped chaeta (San Martín, 2003).

Neurochaetae (73-88). The chaetae can be compound or simple, and unidentate or bidentate (Figs. 8G-J, 9A-H), and similar or unlike on anterior or posterior chaetigers. All this posibilities have been coded as different characters since it is possible to find any combination. The presence of simple chaetae in Syllidae (Figs. 8G, H) might well appear after a fusion process between shaft and blade and could be interpreted as a

secondary acquisition related to a symbiotic life style with other groups of organisms (sponges or corals) (Martín and Britayev, 1998; San Martín, 2003; Musco and Giangrande, 2005; Aguado *et al.,* submitted). Therefore, assuming that simple and compound chaetae could be homologous, the characters 79-84: chaetae unidentate or bidentate and the shape of teeth in bidentate chaetae have been coded for all the species included herein (with simple and/or compound chaetae). However, there is no evidence of a fusion process between fangs and blades in *Bollandia* (Figs. 6K, L), and hence, the characters related to the spinulation of blades have been coded as "inapplicables". Although it is possible to distinguish differences in the articulation and length of dorsal cirri between the anterior, midbody and posterior part of the syllids' body, this regionalization is not so evident in the shape and size of the chaetae. Midbody and posterior chaetae were practically similar in most cases and the changes, when they occurred, were very gradual. Thus, we considered only two groups of characters related to the chaetae (on anterior and posterior segments). The genera *Astreptosyllis*, *Streptosyllis* and *Streptospinigera* present anterior chaetae markedly different in shape and size to the rest (Figs. 9G, H).

The articles of compound chaetae can be all similar or they can show differences in size between anterior and posterior segments, and/or also within the same fascicle. When there are differences in size within same fascicle, they are commonly gradiating in length from dorsal to ventral blades (Fig. 9A). Some genera, such as *Paraehlersia*, *Exogone*, *Erinaceusyllis*, *Streptospinigera*, and some species of *Syllis*, *Dentatisyllis* Perkins, 1981 and *Opisthodonta* present chaetae markedly longer than the rest (Figs. 9C, E). They are called *pseudospinigers* or *spiniger-like* because they remind the long chaetae typical of other families, such us Nereididae. When present, the rest of the blades are considerably shorter and they are called falcigers (Figs. 9C, D, F). *Brania* and *Parapionosyllis* have chaetae ending in an expanded and rounded tip (Fig. 6J). The size of teeth has been also considered. Distal tooth can be larger than proximal one (Fig. 9D), the opposite condition can be found (Fig. 9F), or both teeth can be similar. The distal teeth in *A. acrassiseta* and *Streptosyllis websteri* appear in two different levels instead of being in the same level as in the rest of terminals (Fig. 7D). In some species anterior chaetae have spines on margin, while they are practically smooth on posterior segments. In these cases, we have considered that spines are present since the absence

of this feature might be a secondary loss. Finally, shafts are chambered in Chrysopetalidae and Nereididae (Perkins, 1985).

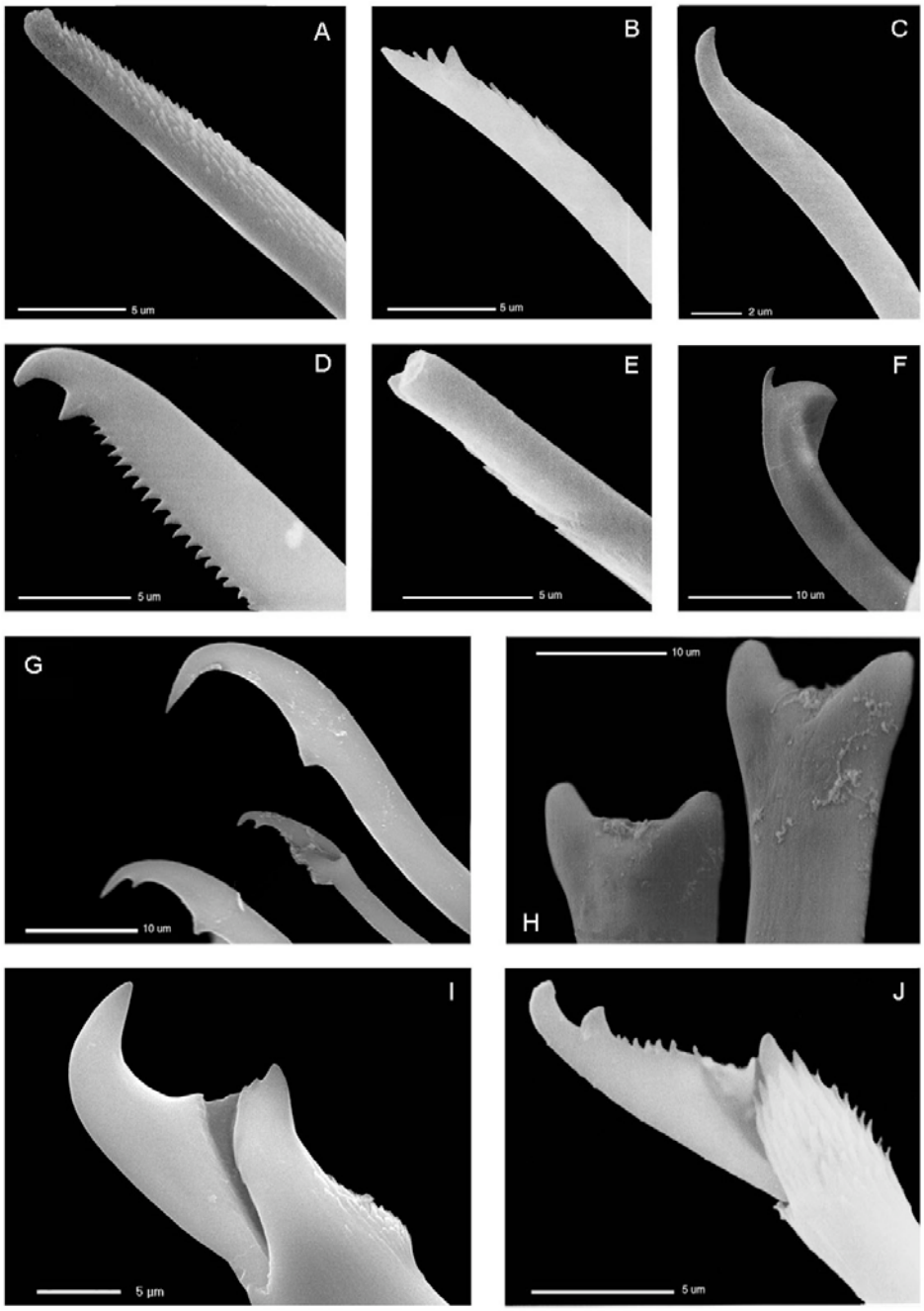

Figure 8. A, *Syllis krohnii*, simple dorsal chaeta (San Martín, 2003); B. *Parapionosyllis minuta*, simple dorsal chaeta (San Martín, 2003); C. *Parapionosyllis minuta,* simple ventral chaeta (San Martín, 2003); D. *Syllis krhonii*, simple ventral chaeta (San Martín, 2003); E. *Pionosyllis weismanni*, simple dorsal chaeta (San Martín, 2003); F. *Pionosyllis weismanni*, simple ventral chaeta (San Martín, 2003); G. *Alcyonosyllis exiliformis*, midbody chaetae (Aguado *et al.*, submitted); H. *Syllis gracilis*, posterior chaetae (San Martín, 2003); I. *Branchiosyllis maculata*, midbody chaeta (San Martín *et al.*, in press); J. *Odontosyllis fulgurans*, anterior chaeta (San Martín, 2003).

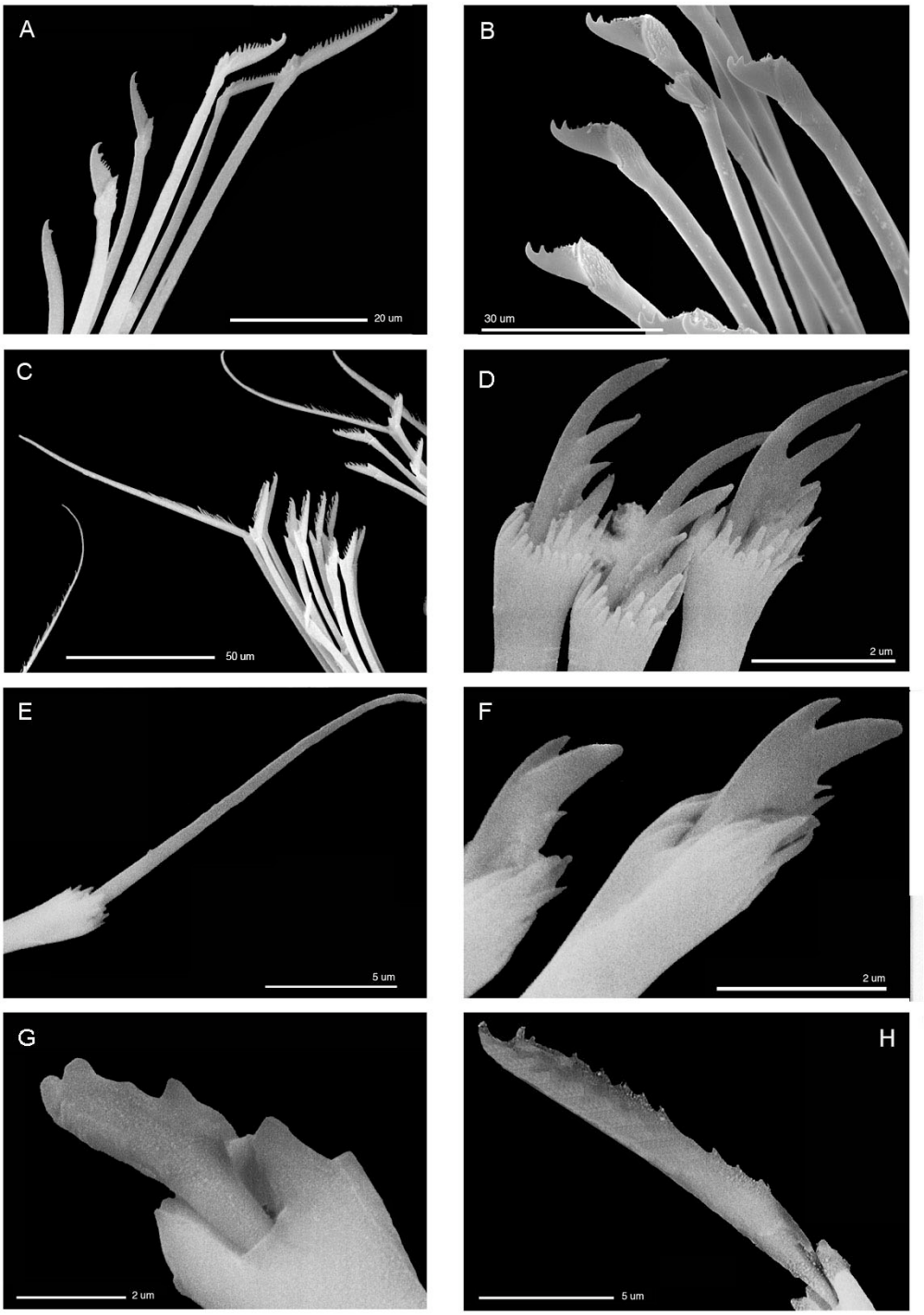

Figure 9. A, *Syllis rosea*, posterior chaetae (San Martín, 2003); B. *Odontosyllis undecimdonta,* midbody chaetae (Aguado *et al.*, submitted); C. *Syllis garciai*, midbody chaetae (San Martín, 2003); D. *Exogone naidina*, anterior chaetae (San Martín, 2003); E. *Exogone naidina*, anterior pseudospiniger chaeta (San Martín, 2003); F. *Exogone naidina*, posterior falcigers, (San Martín, 2003); G. *Streptosyllis campoyi*, anterior chaeta (San Martín, 2003); H. *Streptosyllis campoyi*, posterior chaeta (San Martín, 2003).

Proventricle (89-91). The proventricle has been proposed as the synapomorphy of Syllidae (Glasby, 1993) (Figs. 1B, 10A, B). However, a similar structure has been found in other families, such as Sphaerodoridae. *Sphaerodoropsis anae* possess a proventricle quite similar in its general structure and distribution of muscular cells (Aguado & Rouse, 2006). We have not compared histologically the two structures, but since they look like quite similar externally, *Sphaerodoropsis* has been coded as having proventricle. *Bollandia* was described with a short and barrel-shaped proventricle, although we could not verify this character since the paratypes revised were opaque and could not be dissected. This species has been coded according to Glasby (1994). In some genera of Exogoninae, the proventricle is remarkably wide and short, being almost spherical, whereas it is normally cylindrical in most of syllids (Figs 9A, B). We considered that the proventricle was long when it occupied more than three segments, short when it occupied less than three segments and very long when it occupied a high number of segments (usually more than eight).

Pharynx (92-95). The innermost part of the pharynx is lined with a chitinous layer in Syllidae (Perkins, 1987). This character was also used by Nygren (1999) and by Pleijel & Dahlgren (1998). The latter authors observed that it was also present in *Sphaerodorum gracile* (Rathke, 1843); however we are not sure about its presence in *Sphaerodoropsis anae*, subsequently it has been coded as unknown. The length of pharynx is related to the length of proventricle, and therefore it is an inapplicable character for the outgroup, except for *Sphaerodoropsis*. We have considered that the pharynx is broad when it is almost as wide as the proventricle and very narrow when it is half the width of the proventricle. The pharynx is conspicuously long, very narrow and sinuous in Autolytinae (Fig. 6C), *Amblyosyllis* and *Parahaplosyllis* Hartmann-Schröder, 1990; it is short and wide in *Prosphaerosyllis* San Martín, 1984 and *Salvatoria. Bollandia* was described with a sinuous pharynx and lacking pharyngeal armature (Glasby, 1994).

Pharyngeal armature (96-101). In syllids, there are three different chitinous pharyngeal armatures. The first kind is a unic pharyngeal tooth normally located in the anterior margin of the pharynx (Figs. 10C, D), although it can be positioned in the middle to posterior part (in *Opisthosyllis* and most species of *Opisthodonta*, *Psammosyllis* Westheide, 1990 and *Prosphaerosyllis*). It is always located dorsally within the

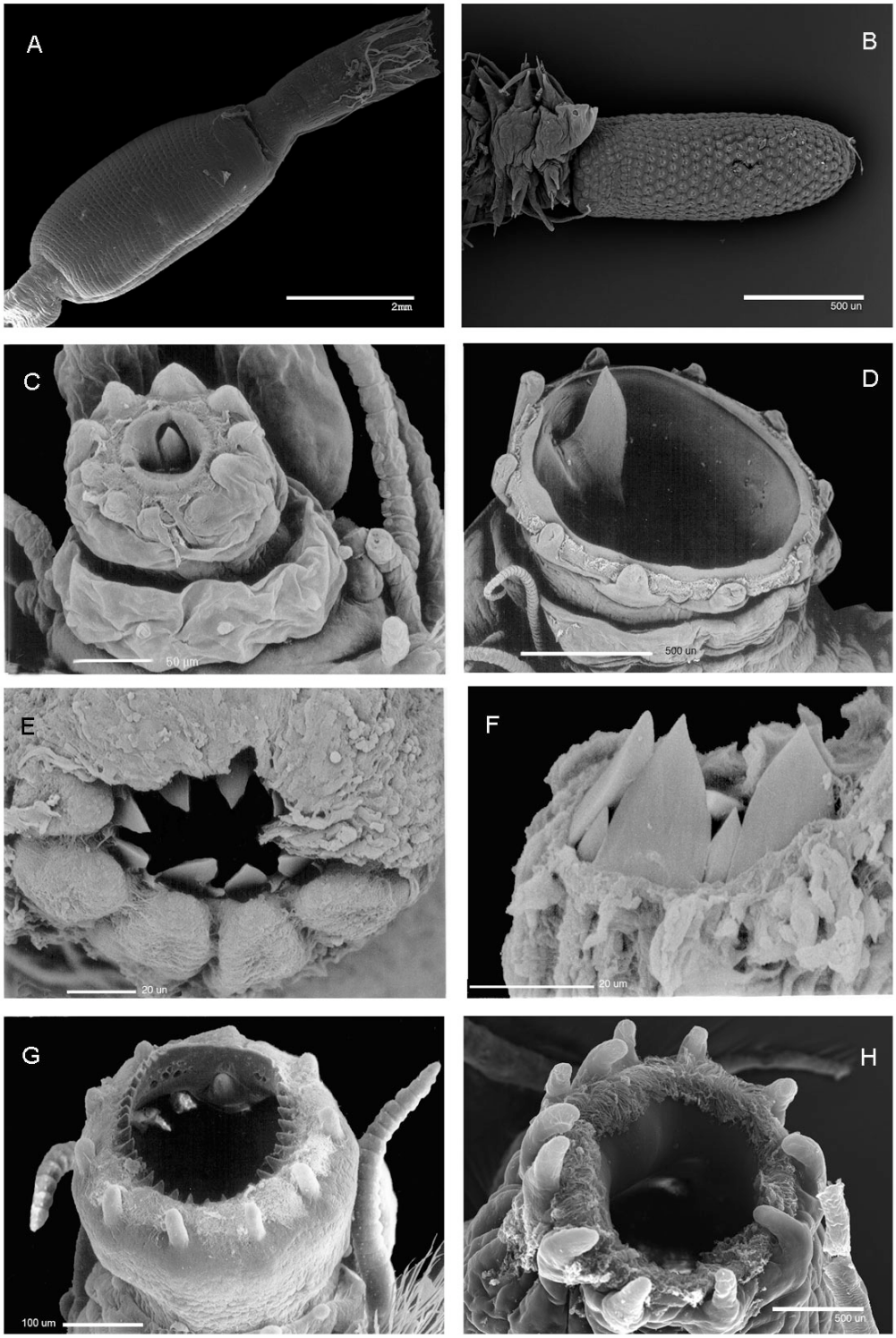

Figure 10. A, *Syllis inflata*, pharynx and proventricle (San Martín *et al.*, submitted b); B. *Haplosyllides aberrans*, proventricle (Martin *et al.*, submitted); C, *Syllis gerundensis*, everted pharynx and pharingeal tooth (San Martín, 2003); D. *Haplosyllis spongicola*, everted pharynx and pharingeal tooth (San Martín, 2003); E. *Proceraea picta*, trepan (San Martín, 2003); F. *Proceraea picta*, detail of trepan (San Martín, 2003); G. *Eusyllis assimilis*, denticled arc (San Martín, 2003); H. *Haplosyllides aberrans*, everted pharynx (Martin *et al.*, submitted).

pharynx, and it is usually conical, although sometimes rhomboidal (in *Cicese*, *Erinaceusyllis*, *Salvatoria* and *Prosphaerosyllis*). A pharyngeal tooth is present in most of the genera of Syllinae, Exogoninae and Eusyllinae and absent in Autolytinae, *Amblyosyllis*, *Inermosyllis* San Martín, 2003, *Murrindisyllis*, *Xenosyllis*, *Nooralia*, *Streptosyllis*, *Astreptosyllis*, *Streptospinigera* and *Syllides* (Fig. 10H). Genera *Haplosyllides* and *Trypanosyllis* present pharyngeal tooth only in the juvenile stages, lacking in adults (San Martín *et al.*, 1997; San Martín, 2003). In these cases it has been coded as present. A second possibility is having a ring of chitinous teeth in the whole margin of the pharynx. This structure, called trepan (Figs. 10E, F), is present in Autolytinae, *Amblyosyllis*, *Trypanosyllis*, *Eurysyllis* and *Trypanoseta* Imajima & Hartman, 1964 (in some Syllinae genera a pharyngeal tooth is also present in addition to the trepan). The third kind of pharyngeal armature is a ventral denticled arc (a series of small teeth located only on the ventral margin of the pharynx) (Fig. 10G), which is present in *Dioplosyllis*, *Brachysyllis*, *Odontosyllis*, *Eusyllis* and *Miscellania* Martin, Alós & Sardá, 1990. None of these three kinds of armature are present in the outgroup terminals. Nereididae, Chrysopetallidae and Pisionidae have jaws, which are not chitinous. *Sphaerodoropsis anae* has not any pharyngeal armature.

Reproduction (102-110). Most of syllids and also *Neanthes* suffer several modifications in their bodies for reproduction. These modifications are different on each subfamily and they have been traditionally considered as two distinct reproductive modes: epigamy and schizogamy (see the introduction). In both modes notochaetae are developed (Fig. 11A). Some syllids developed other reproductive systems being viviparous (*Dentatisyllis*, *Parexogone hebes* between others) and transferring sperm directly (*Neopetitia*) (Ding *et al.*, 1998; Bührmann *et al.*, 1996a, 1996b). These modifications have been considered as adaptations to the interstitial way of life (Westheide, 1990). In these cases, there is no modification in the parental body.

Schyzogamy could be divided into scissiparity and gemniparity. However, gemmiparity (Fig. 1A) is only present in *Myrianida* Milne Edwards 1845 being an apomorphy of this genus (Nygren, 2004), an autapomorphy herein, and therefore it has not been included in the present analyses. Scissiparity can further be divided into anterior scissiparity, where the single stolon is formed behind character 13, and posterior scissiparity, where the stolon is formed at a more posterior and variable position (Nygren & Sundberg, 2003). The stolons are different in Syllinae and

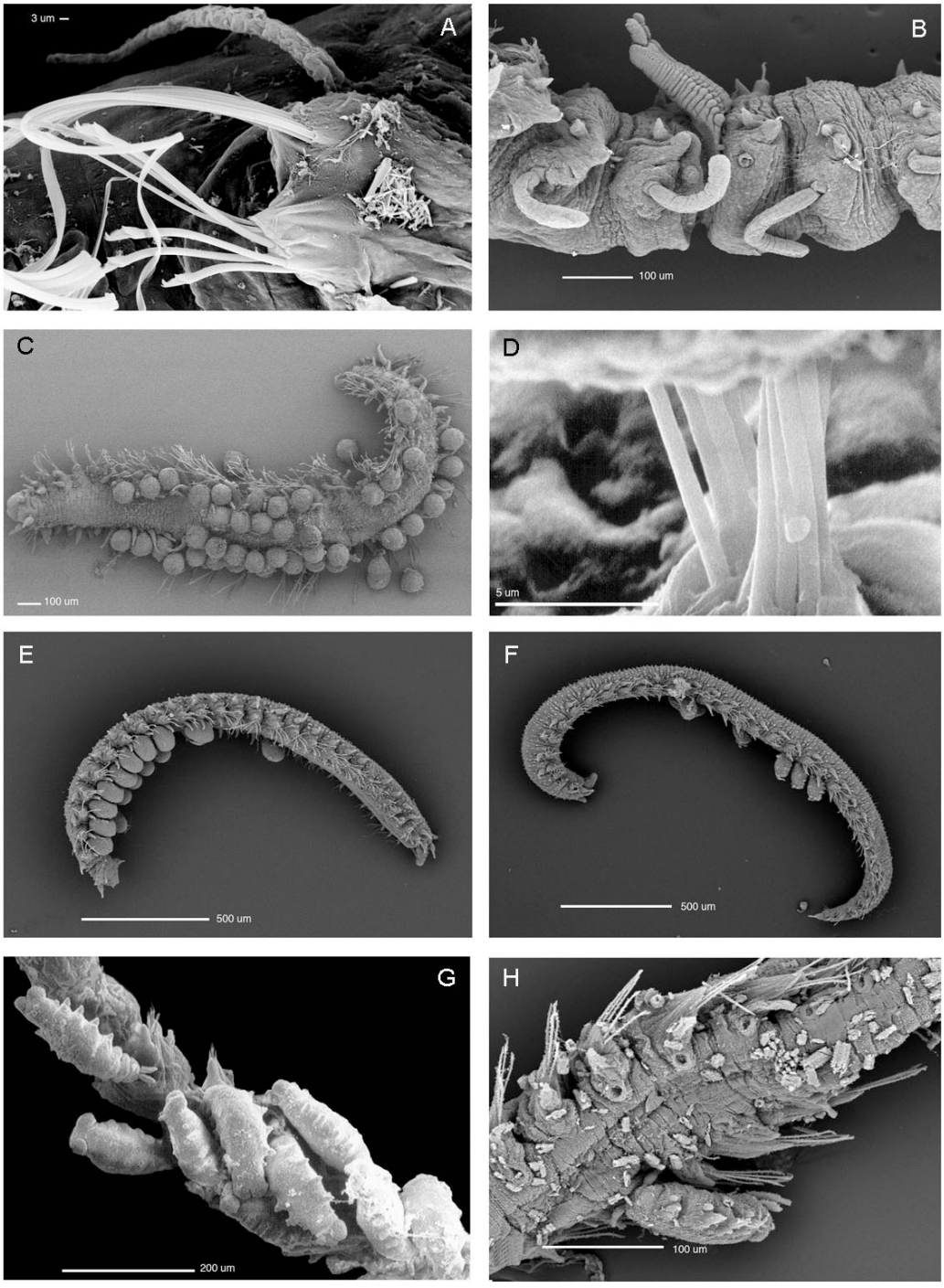

Figure 11. A, *Paraehlersia ehlersiaeformis*, midbody parapodium of epigamic specimen (San Martín & Huchings, 2006); B. *Alcyonosyllis glasbyi*, stolon in formation and posterior end regenerating (San Martín, in prep.); C, *Erinaceusyllis erinaceus*, dorsal view (Aguado & San Martín, in prep.); D. *Salvatoria vieitezi*, notochaetae attached to egg (San Martín, 2003); E. *Sphaerosyllis hirsuta*, mature female carrying eggs, lateral view (San Martín, 2005); F. *Sphaerosyllis hirsuta*, mature female carrying juveniles, lateral view (San Martín, 2005); G. *Exogone verugera*, mature female carrying juveniles (San Martín, 2003). H, *Exogone africana*, detail of a female carrying juveniles, ventral view (San Martín, 2005).

Autolytinae. In Autolytinae (Fig. 1C), they are regionalized in three different parts and with a clear sexual dimorphism, while they are not differentiated in Syllinae (1D). In Autolytinae and Syllinae, stolons are developed in the posterior part of the body and become active swimmers when they are completely developed and detached. In Syllinae, after this process, many species regenerates the posterior segments (*Syllis, Opisthosyllis, Trypanosyllis,* etc). The regeneration of the posterior segments occurs before the separation of the stolon in some genera. In these cases, the stolon is attached dorsally to the parental body (Fig. 11B) and develops while it regenerates its posterior part. It has been reported for *Nuchalosyllis* (Aguado & San Martín, in press), *Alcyonosyllis* (Glasby & Watson, 2001, San Martín & Nishi, 2003 and Aguado *et al.*, submitted), *Parahaplosyllis* (pers. obs.) and some species of *Trypanosyllis* (San Martín, 2003).

The Exogoninae genera *Prosphaerosyllis*, *Salvatoria*, *Erinaceusyllis* and *Cicese* show dorsal brooding (Figs. 11C, D); while genera *Exogone*, *Parapionosyllis*, *Sphaerosyllis* and *Brania* present ventral brooding, (Figs. 11E-H). The enigmatic genus *Nooralia* (assigned, although with doubts to Exogoninae) show a third kind of brooding carrying eggs attached to the compound neurochaetae (San Martín, 2002). It has been coded herein as a dorsal brooder. In Eusyllinae, some genera as *Nudisyllis pulligera* (Krohn, 1852) and *N. tinihekea* Knox & Cameron, 1970 also brood eggs attached to dorsal cirri. Others do it in ventral position, such as *Syllides japonicus* Imajima, 1966, *Syllides benedicti* (Banse, 1921) and *Pionosyllis augeneri* (Hartmann-Schröder, 1979) (the two latter not included in the analyses) (Heacox & Schroeder, 1978; Hartmann-Schröder, 1979 and per. obs.). Different genera brood eggs in gelatinous masses (*Amblyosyllis speciosa* Izuka, 1912 and *Anoplosyllis edentula* Claparède, 1868) (Pernet, 1998; Cognetti-Varriale, 1971). Some species of genera *Epigamia*, *Myrianida*, *Procerastea* and *Proceraea* Ehlers, 1864 brood eggs in ventral sacs (Berkeley, 1923; Hamond, 1937; Okada, 1933; 1937; Cognetti, 1953; Gidholm, 1965; Franke, 1999; San Martín, 2003). In this study, we have considered viviparity as an additional kind of brooding.

Most of syllids have a plancktonic development, but the larval stage has been substituted by a direct development. It occurs in the Exogoninae genera where juveniles are attached ventrally to parental bodies (Pierantoni, 1903; Potts, 1911) (Figs. 11E-G). *Nudisyllis pulligera* also exhibit direct development carrying the embrios on dorsal cirri, and in *Dentatisyllis* and *Parexogone hebes,* embrios are developed within the parental

body. The reproductive mode of two terminals (*Brachysyllis infuscata* Ehlers, 1901 and *Streptospinigera heteroseta* Kudenov, 1983) is unknown, although it is well known in other species of same genera, respectively. Both species have been coded as epigamic, assuming that they have the same reproductive mode as other similar species in their respective genera. *Amblyosyllis* has been considered an epigamic species (Aguado *et al.*, submitted), although Pernet (1998) described specimens without swimming chaetae brooding in gelatinous masses. We have considered this species as epigamic but also brooding in gelatinous masses.

Postembrionic development (111). We were only able to include one character about changes in the morphology during the animal's life. The species *Eusyllis blomstrandi* and *Paraehlersia ferrugina* have completely smooth dorsal cirri when they are juveniles, but they become pseudoarticulated when they are adults.

Morphological characters not used

A number of features commonly used in syllid descriptions have not been implemented herein. Some of them principally because there has not been systematic documentation of these structures across the group. That is the case of the presence of spiral glands in dorsal cirri and glands in the epidermis. The latter feature has been properly described only for some genera, such as *Haplosyllides* and several Autolytinae (San Martín *et al.*, 1997; Nygren, 2004; Martin *et al.*, submitted). The presence of antenophores and differences in length of cirrophores might be other informative characters but they are also very difficult to discern in preserved material. Finally, the presence of a terminal ring of cilia on the pharynx and one or two rings of terminal papillae are characters not uniformally described in all the species.

Other characters considered in a previous phylogenetic analysis about Autolytinae (Nygren, 2004), were not included herein because its presence is not applicable or well known for the rest of syllids. That is the case of the existance of red spots on the base of parapodia, number of sinuations in pharynx and details of the trepan, characters about the raphes (i. e. the two sutures which divide the proventricle) and shape, number and size of muscular elements in the proventricle. Haswell (1921) considered that the ventricle was absent in Autolytinae, but we could not confirm this hypothesis. It was also not considered by Nygren (1999, 2004).

Other characters, such as dorsal cirri orientation, were not included since they necessary force the study of fresh material, not always available. The ciliary bands on embrios, as well as the characters related to the epitokes might be very interesting but the information is still very scarce for the group. In general, all these features have been poorly studied and should receive more attention in the future.

Phylogenetic analyses

The parsimony analyses were performed in PAUP* 4.0b10 (Swofford, 2002) in combination with PAUPRat "Paup*implementation of the parsimony ratchet" (Nixon, 1999), betaversion 1 (Sikes and Lewis, 2001). Each ratchet analysis was run for 3000 replicates with default settings. All characters were left unweighted and non-additive. Clade support was assessed using Bremer support (B) (Bremer, 1998) calculated in TNT (Goloboff *et al.*, 2004) and parsimony jackknifing (Farris *et al.*, 1996) calculated in PAUP. Jackkniffe values (JK) were calculated from 1000 replicates, heuristic searches, 37% character deletion, TBR, and 3 ramdom additions. Strict consensus, retention indices (RI) and consistency indices (CI) were calculated with PAUP. We used ACCTRAN optimization to examine character evolution.

RESULTS

First analysis: including one species of all the valid genera

The Parsimony analysis performed in PAUPratchet yielded 155 most-parsimonious trees with 635 steps long, CI: 0.246 and RI: 0.627. The strict consensus is shown in Fig. 12 and the first most parsimonious tree in Fig. 13.

The resulting strict consensus (Fig. 12) includes a monophyletic clade in which all the syllid genera are contained but also the outgroup *Sphaerodoropsis anae*. This clade is a large polytomy not highly suported (4B, 65JK) and principally defined by the presence of the proventricle. Some other features also support this large polytomy: the presence of a chitinous inner proboscis (unknown for *S. anae* and *Bollandia*); conical palps (a reversial for *S. anae*); palps with some degree of fussion (reversials in *Nuchalosyllis*, *Xenosyllis*, *Plakosyllis*, *Parahaplosyllis*, *Brachysyllis* and *Eusyllis*); and

it is also characterized by the absence of two features common in most of outgroups: jaws and notoacicula.

Within the large polytomy, there are four monophyletic groups. From up to down, the first monophyletic group comprises five genera traditionally assigned to Eusyllinae and it is labelled herein as Clade I, the second clade containes all the Exogoninae genera, the third one all the Autolytinae plus *Bollandia*, and finally, the fourth includes several Eusyllinae members and all the Syllinae. The genera *Anguilosyllis*, *Miscellania*, *Murrindisyllis*, *Neopetitia*, *Nooralia* and *Psammosyllis* appear misplaced in the consensus (Fig. 12).

Clade I is well supported (8B, 74JK) and includes *Anoplosyllis edentula*, *Syllides japonicus*, *Streptosyllis websteri*, *Astreptosyllis acrassiseta*, and *Streptospinigera heteroseta*. It is defined by one uncontradicted apomorphy: ventral cirri medially inserted; and two apomorphies with reversials and parallelisms: presence of granules on the dorsum of peristomium (which is a reversial in *Astreptosyllis* and *Streptospinigera*) and the absence of pharyngeal tooth (in common with several groups, such as Autolytinae, *Murrindisyllis*, *Nooralia*, *Odontosyllis*, *Anguillosyllis*, *Anoplosyllis*, *Bollandia*, *Amblyosyllis*, *Xenosyllis*, *Inermosyllis* and *Trypanosyllis*). Within Clade I, the group *Syllides-Streptospinigera* is well supported (7B, 80JK) and presents several apomorphies with reversals and homoplasies: dorsal cirri with a fixed pattern of articulation (not shared *by Streptosyllis websteri* although it is present in other species of the same genus), presence of impair anal appendix (in common with *Dentatisyllis*, *Syllis*, *Murrindisyllis* and *Neopetitia*), and presence of dorsal simple chaetae from anterior segments (convergency with Autolytinae, Exogoninae, *Murrindisyllis*, *Miscellania*, *Neopetitia* and *Nooralia*). The following clade: *Streptosyllis-Streptospinigera* is supported by high values (8B, 81JK) and one uncontradicted apomorphy: anterior dorsal simple chaetae modified on anterior segments; and three parallelisms: posterior ventral cirri elongated (in common with *Palposyllis*), anterior chaetae different to midbody and posterior ones (in common with *Nooralia*), and anterior aciculae enlarged (under an ACTRANN transformation) (reverting in *Astreptosyllis* and in common with *Streptodontha*). Finally, the clade comprising *Astreptosyllis* and *Streptospinigera* (7B, 64JK) is not defined by any clear apomorphy.

In the first MPT (Fig. 13) the Clade I is the sister group of the large clade that contains most of Eusyllinae members and Syllinae.

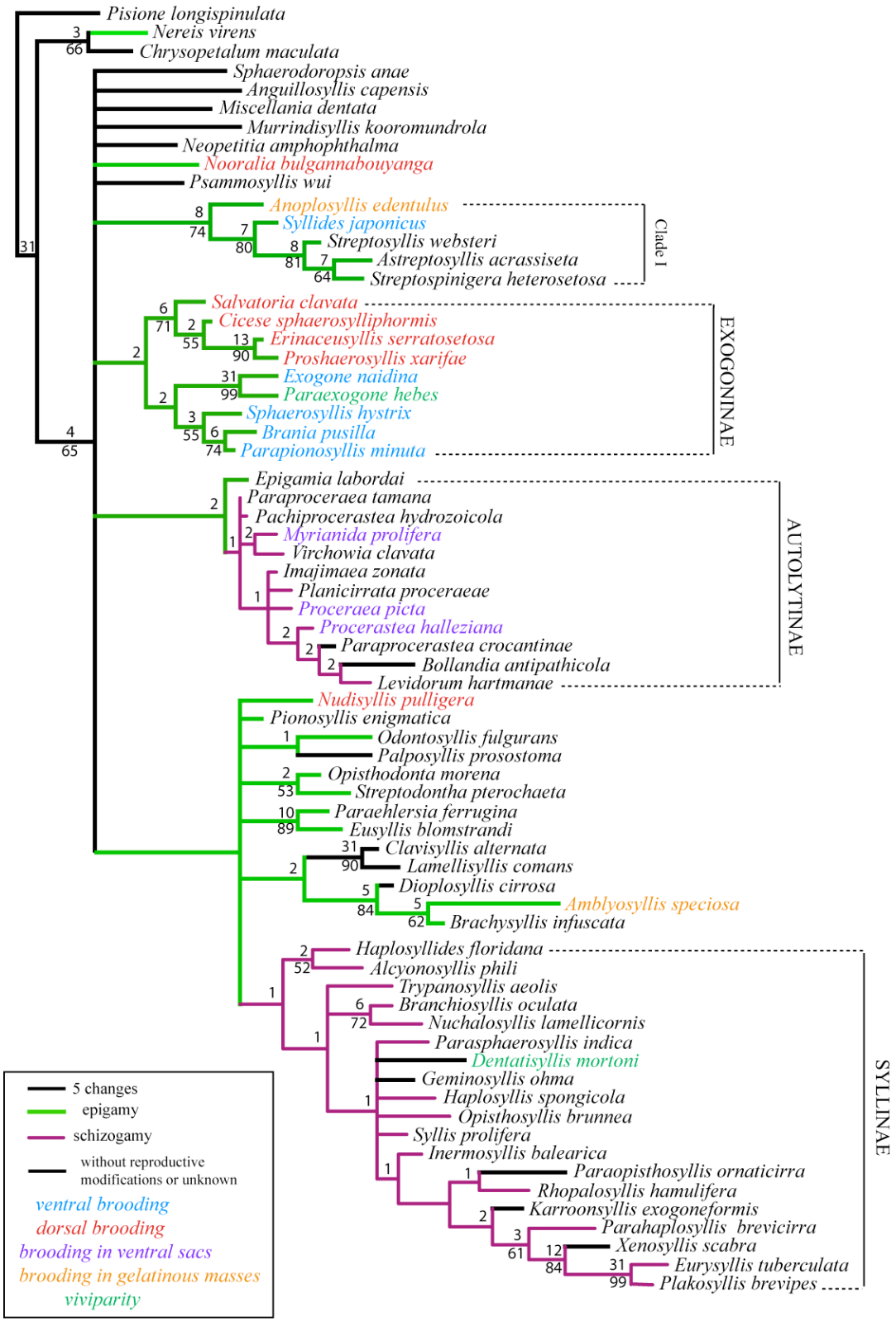

Figure 12. Strict consensus of the first morphlogical analysis including all the genera in Syllidae.

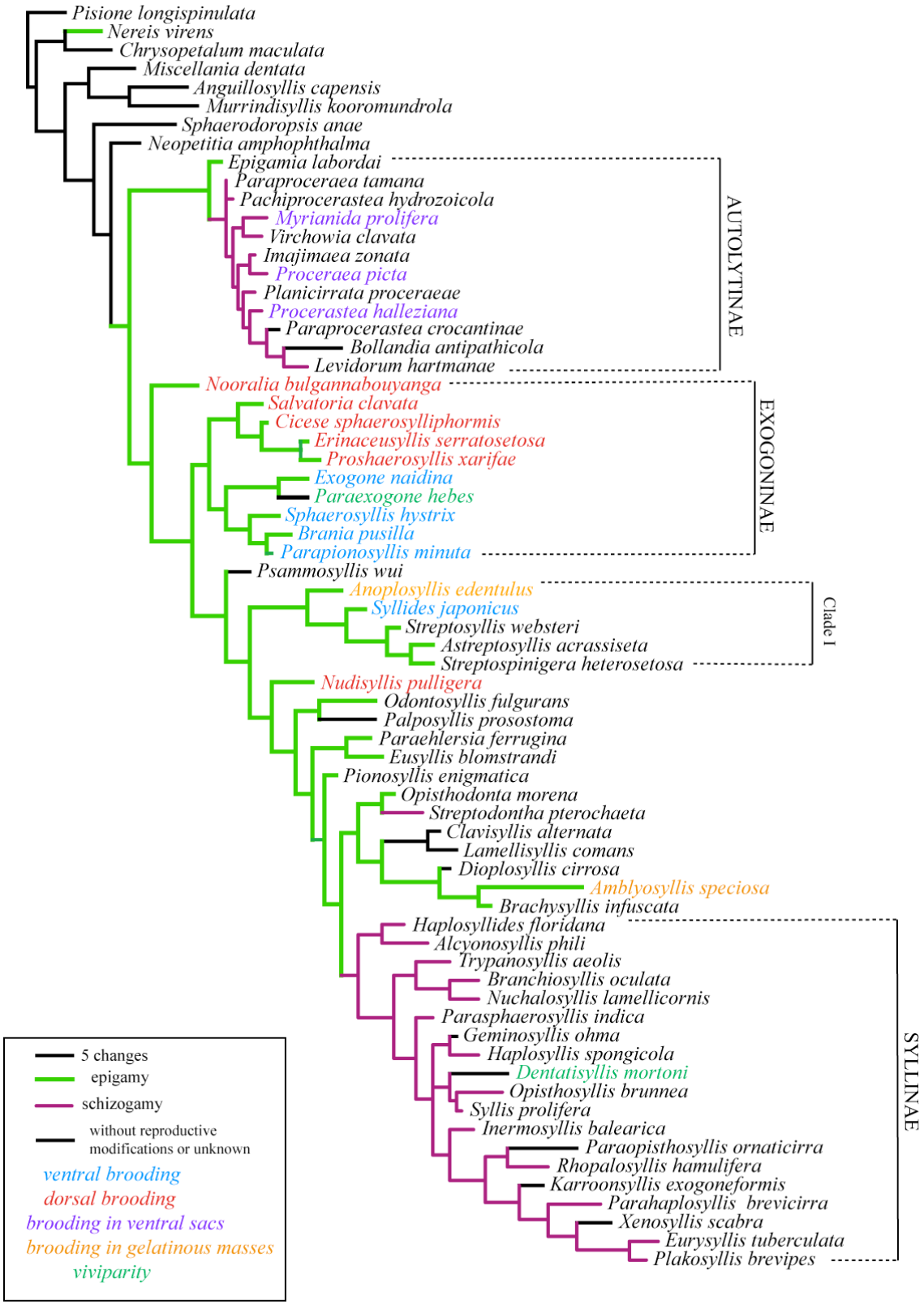

Figure 13. First most parsimonious tree obtained from the first morphlogical analysis including all the genera in Syllidae.

The following large clade contains all the genera traditionally assigned to the subfamily Exogoninae. It is not well supported (2B) and has only one uncontradicted apomorphy: the shape of anal cirri. The group also shows several apomorphies with multiple reversials within the clade: shape of antennae (in common with *Chrysopetalum* Ehlers, 1864 and *Miscellania*), onion shaped or fusiform dorsal cirri (in common with *Chrysopetalum*), changed to papilliform dorsal cirri in *Exogone* and *Parexogone*; presence of dorsal simple chaetae from the anterior segments (this character is shared with same groups as *Astreptosyllis-Syllides* clade); and the palps totally or practically fused (in common with Autolytinae, *Eurysyllis*, *Karoonsyllis*, *Anguillosyllis*, *Murrindisyllis* and *Psamosyllis*), which changes to basally fused in *Brania* and *Parapionosyllis*.

Exogoninae is also characterized by the dorsal/ventral brooding of eggs (in common with *Nudisyllis*, *Syllides*). Within the Exogoninae clade, there are two clear and well-supported groups. The first one (2B) contains all the Exogoninae genera that brood ventrally (including *Parexogone hebes*, for which this kind of brooding is modified to viviparity); and the second one (6B, 71JK), which includes all the Exogoninae genera that carry eggs dorsally (in common with *Nooralia*), and the presence of a rhomboidal pharyngeal tooth. Both clades are subsequently divided in different groups. Within ventral brooders, *Sphaerosyllis*, *Brania* and *Parapionosyllis* (3B, 55JK) have parapodial glands opened by pores. *Brania* and *Parapionosyllis* (6B, 74JK) have the aciculae distally hollow (a parallelism with *Opisthosyllis brunnea* and *Syllis prolifera* Krohn, 1852) and their falcigers ending in a rounded tip. *Exogone* and *Parexogone* (31B, 99JK) share the shape of antennae, "tentacular" and dorsal cirri. On the other hand, within the dorsal brooders, *Cicese*, *Erinaceusyllis* and *Prosphaerosyllis* (2B, 55JK) share the apomorphies: presence of papillae over dorsum (in common with *Sphaerodoropsis*, *Xenosyllis*, *Rhopalosyllis*, *Trypanosyllis*, *Sphaerosyllis*, *Paraopisthosyllis* and *Palposyllis*); prostomium retractile under peristomium (a parallelism with *Sphaerosyllis* and *Exogone*); and lateral wings on perstomium considering an ACCTRAN transformation (reverting in *Prosphaerosyllis*). *Erinaceusyllis* and *Prosphaerosyllis* (13B, 90JK) do not reveal any clear apomorphy.

The third large clade is not well supported (2B) and comprehends all the genera traditionally assigned to Autolytinae plus the enigmatic genus *Bollandia*. Several

morphological features define this clade, two of them, such as reduction of ventral cirri and dorsal simple chaetae bayonet shaped, are present in all the traditionall Autolytinae genera although they are reversials in *Bollandia*. Other apomorphies with different kinds of homoplasy are: palps reduced or absent (in common with some outgroups, such as *Pisione* and *Sphaerodoropsis*) and ventrally folded (converging with *Clavisyllis* and *Paraopisthosyllis*, *Amblyosyllis*, *Nuchalosyllis*, *Eurysyllis*, *Plakosyllis* and *Rhopalosyllis*); palps totally or practically fused (in common with Exogoninae, *Eurysyllis*, *Karronsyllis*, *Anguillosyllis*, *Murrindisyllis* and *Psammosyllis*); presence of nuchal epaulettes (a parallelism with *Nuchalosyllis*, *Amblyosyllis*, *Clavisyllis* and *Lamellisyllis*); presence of dorsal simple chaetae from anterior segments (in common with other groups as explained for Clade I); anterior and posterior falcigers with proximal tooth larger than distal one (a convergency with *E. naidina* Örsted, 1845, *Eusyllis*, *Paraehlersia*, *Opisthodonta* and *Streptodontha*); presence of a long and sinuous pharynx (a parallelism with *Amblyosyllis* and *Parahaplosyllis*); absence of pharyngeal tooth (in common with same groups as Clade I); and presence of trepan (a parallelism with *Dentatisyllis*, *Parahaplosyllis*, *Trypanoseta*, *Trypanosyllis* and *Amblyosyllis*). *Epigamia* is the sister group of the rest of genera (1B), which are supported by some apomorphies: schyzogamy as the reproductive mode (in common with Syllinae), posterior scissyparity and stolons differentiated in regions and showing a clear sexual dimorphism. The kind of brooding might be in ventral sacs, but information is lacking in most of the terminals. In the first MPT (Fig. 13), *Neopetitia* and *Nooralia* appeared as the sister groups of Autolytinae.

Finally, the fourth large clade comprises several Eusyllinae and all the Syllinae genera. This clade is not supported by any clear apomorphy. Within this clade, some monophiletic groups (*Odonthosyllis-Palposyllis*; and *Opisthodonta-Streptodontha*) are also not defined by any apomorphy. However, *Eusyllis blomstrandi* Malmgren, 1867 and *Paraehlersia ferrugina* (Langerhans, 1881) (10B, 89JK) form a well supported clade defined by an uncontradicted apomorphy related to their postembrionic development. In both species, juveniles have smooth dorsal cirri, while the adults show their anterior dorsal cirri indistinctly articulated or pseudoarticulated. Both species also share the presence of ciliary bands over dorsum (in common with *Dioplosyllis*, *Brachysyllis*, *Bollandia*, *Myrianida*, *Murrindisyllis* and *Odontosyllis*).

Another well supported clade comprises *Lamellisyllis* and *Clavisyllis* (31B, 90JK), who share two apomorphies: elliptical and inflated dorsal cirri, and several parallelisms: presence of nuchal epaulettes (parallelism with most of Autolytinae, *Amblyosyllis* and *Nuchalosyllis*) and a ribbon-shaped body (in common with some Syllinae). This clade is linked (although without support values) with another well supported group (5B, 84JK) that includes the species *Dioplosyllis cirrosa* Gidholm, 1962, *Amblyosyllis speciosa* and *Brachysyllis infuscata*. These three species share four uncontradicted apomorphies: lateral antennae, "tentacular", anterior and posterior dorsal cirri very long; and some more apomorphies with reversials and homoplasy: The presence of dorsal ciliary bands (a reversial in *Amblyosyllis* and a convergence with same species as *Eusyllis* and *Paraehlersia*), very long antennae and midbody dorsal cirri (in common with *Murrindisyllis*), long palps (a reversial in *Amblyosyllis* and homoplasy with *Karroonsyllis*, *Anguillosyllis* and *Palposyllis*), and presence of a ventral denticled arc (in common with *Eusyllis*, *Miscellania* and *Odontosyllis*), which change into a trepan in *Amblyosyllis*. *Amblyosyllis* and *Brachysyllis* are closer to each other in a clade (5B, 62JK) supported by two uncontradicted autopomorphies: segments trapezoidal and the preanal segment without chaetae, and one parallelism: limited number of segments (in common with *Anguillosyllis* and *Miscellania*).

Within the fourth large clade, the last monophyletic group comprises all the Syllinae and also two enigmatic genera previously assigned with doubts to other subfamilies (*Paraopisthosyllis* and *Karroonsyllis*). This clade is poorly supported (1B) by only two apomorphies: anterior scissyparity and stolons without distinct regions and not showing dimorphism. Unfortunately, the reproductive mode is unknown for several terminals. *Alcyonosyllis* and *Haplosyllides* (2B, 52JK) appear as the sister group of the remaining Syllinae genera (Figs. 12, 13) and share the appearance of simple chaetae (in common with several genera in Autolytinae an Syllinae). *Branchiosyllis oculata* and *N. lamellicornis* (6B, 72JK) share the presence on unidentate chaetae on anterior and posterior parapodia. The genera *Eurysyllis*, *Plakosyllis*, *Xenosyllis*, *Parahaplosyllis*, *Karroonsyllis*, *Rhopalosyllis* and *Paraopisthosyllis* constitute a clade defined by two features: body ribbon shaped (a reversial in *Karronsyllis* and a parallelism with *Nuchalosyllis*, *Trypanosyllis*, *Clavisyllis* and *Lamellisyllis*) and presence of antennae, "tentacular", dorsal and anal cirri short, formed by one distinct articulation in *Plakosyllis*, *Xenosyllis* and *Karroonsyllis*. They also share the presence of a short

proventricle (excepting in *Eurysyllis* and *Parahaplosylllis*), while it is long or very long in the rest of Syllinae.

In relation with the reproductive modes, the topography of the strict consensus supports the appearance of schyzogamy twice in the family (in Syllinae and within Autolytinae) as the derived condition from epigamy; the brooding system in *Syllides*, *Nudisyllis* and *Nooralia* as a parallelism with Exogoninae; the brooding system in *Amblyosyllis* and *Anoplosyllis* as a parallelism; and finally, viviparity appearing independently in *Dentatisyllis* and *Parexogone* (Figs. 12, 13).

Second analysis: excluding 19 genera

In the second analysis the number of taxa was reduced in order to decrease the unknown information. Nineteen terminals were excluded because they were poorly known, with many question marks in the first matrix, and consequently most of them appeared in ambiguous positions in the first results. In addition, a majority are monotypic genera, being impossible to obtain information from any other representatives of same genus. The excluded terminals are shown in green in Table 2. This second parsimony analysis yields 23 most parsimonious trees with 464 steps long, CI: 0.328 and RI: 0.652. The strict consensus calculated in PAUP is shown in Fig. 14.

The strict consensus (Fig. 14) shows Syllidae as a monophyletic group, very well supported (15B, 86JK) with *S. anae* as its sister group. The shape of palps defined Syllidae this time. Within Syllidae, same groups as those in the first analysis remain as monophyletic and all of them very well supported. Apomorphies for each group are the same as in the first analysis. The topography of this second consensus shows a more resolved distribution of clades than in the first consensus. Instead of having a large politomy, this hypothesys showed the clade *Amblyosyllis-Dioplosyllis* (7B, 82JK) as the sister group of the rest of syllid genera organized in a second clade. Within this clade, there are two groups. The first one comprises the Clade I, Autolytinae and Exogoninae; and the second one includes some Eusyllinae genera and Syllinae. The relationships between genera within the Clade I are the same than those found in the first analysis. In contrast, within Autolytinae, *Epigamia* does not remain as the sister group of the rest of terminals; it appears as a derived genus with a reversal in the reproductive mode. Within Exogoninae, same monophyletic groups as in the first analysis are shown: the dorsal

brooders (*Salvatoria-Prosphaerosyllis*; 21B, 78JK), and the ventral brooders (*Exogone-Sphaerosyllis*; 6B, 54JK). Within Syllinae, one additional monophyletic group appears: *Inermosyllis*, *Opisthosyllis*, *Dentatisyllis* and *Syllis* (5B), defined by the presence of spines in ventral simple chaetae (in common with *B. pusilla*, *S. clavata* and *O. fulgurans*). The topography of this strict consensus also supports same results about the evolution of the reproductive modes and brooding modes than the first analysis.

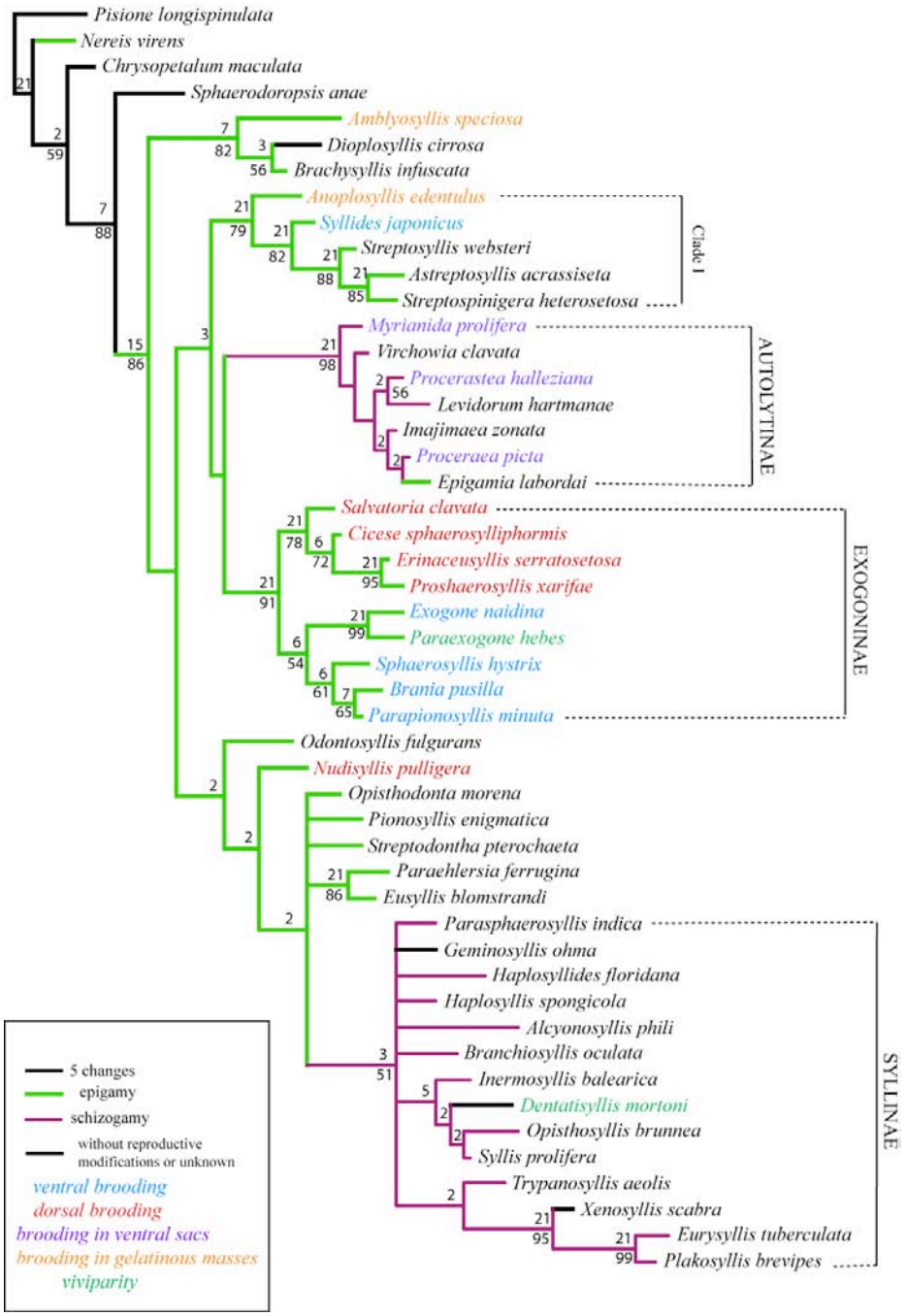

Figure 14. Strict consensus of the second morphological analysis excluding 19 genera.

In order to obtain a better resolution of the results (principally in the first analysis) and also to compare and contrast the meaning of the morphological knowledge about syllids, different codification systems were also tested transforming the above-described characters in other codification schemes. Firstly, we transformed all the information in absent-present or binary characters (the "D" method, sensu Pleijel, 1995). In other analyses we considered multistate characters, also including the absences as an additional state on each complex character ("A" and "B" methods, s. Pleijel, 1995 and the composite coding s. Strong & Lipscomb, 1999). We also reduced the number of states in some characters maintaining same number of terminals. Nautiliniellidae and Pilargidae were considered as additional outgroups in previous analyses. Other additional attempts considered different interpretations for some taxa. For instance, the consideration of the lateral macrotubercles in *Sphaerodoropsis anae* as dorsal cirri, or the simple chaetae in *Pisione* as different to the simple dorsal and ventral simple chaetae in syllids, as well as different interpretations of some features in *Bollandia* (see below). Finally, an analysis including all the possible polymorphisms in the characters was also performed. Any of these variations from the described characters, ingroup and outgroup resulted in practically same results or even less resolved and consequently, they are not included herein.

DISCUSSION

This study represents the first attempt to elucidate the phylogenetic relationships between all the genera of Syllidae with cladisitic methodology. Because the results are ample and their discussion complex, the following paragraphs have been organized in different parts to ease their reading. The well supported monophyly of the principal groups is firstly discussed, and is then followed by a discussion about the evolutionary relationships between the reproductive modes and the different brooding systems displayed by the family. Thereafter, the similarities between Syllidae and Sphaerodoridae are discussed, focusing most attention in the proventricle and arguing how this structure may be related with the reproductive modes of Syllidae. Next, the particularities of this study are confronted with observations made in previous reports, and the possible organization of Eusyllinae is then discussed. Since *Bollandia* is an unusual organism we considered it needed its own (small) paragraph, and then the

evolution of some morphological characters is discussed in more detail. Finally, the possible causes underlying the lack of resolution when including all the genera are exposed.

The results presented herein (i.e. the first and second analyses), are congruent among them as well as with previous studies published elsewhere (Nygren, 1999; Nygren & Sundberg, 2003; Aguado *et al*., 2007). They contain monophyletic groups within Syllidae and, in general terms, equivalent hypotheses about the evolution of the reproductive modes. Within Syllidae the traditional subfamilies Autolytinae, Syllinae and Exogoninae are shown as monophyletic (although the level of support varies upon which is the analysis), while Eusyllinae is resolved as paraphyletic (in agreement with Nygren, 1999; Nygren & Sundberg, 2003 and Aguado *et al*., 2007). In addition, *Anoplosyllis*, *Astreptosyllis*, *Streptosyllis*, *Syllides* and *Streptospinigera* represents another well-supported monophyletic group (called in this paper Clade I), coinciding with the results of Aguado *et al*. (2007), and also with the suggestion of Licher (1999), the latter which nonetheless was not based on phylogenetic grounds. Results also address that the genera *Brachysyllis*, *Amblyosyllis* and *Dioplosyllis* can be a monophyletic group, the two latter genera were also found to be a strongly supported clade in Aguado *et al*. (2007).

The consensus topologies (Figs 12, 14) suggest epigamy as the primitive reproductive mode and that schyzogamy has appeared twice, in Syllinae and Autolytinae, all of which is in agreement with previous studies (Nygren, 1999; Nygren & Sundberg, 2003; Aguado *et al.*, 2007). The Schyzogamy in Autolytinae and Syllinae could be considered as the by-product of different processes with independent origins since in both clades they differ in characteristics such as the regionalization and the sexual dimorphism of stolons (Garwood, 1991). Within Exogoninae the monophyly of ventral and dorsal brooders was supported by both morphological analyses and by the molecular results of Aguado *et al*. (2007), as well as by the suggestions made in previous non cladistic studies (Mastrodonato *et al*., 2007; San Martín, 2003, 2005). Brooding care in *Syllides* and *Nudisyllis* might be a parallelism and brooding in ventral egg sacs seems to occur only in Autolytinae (both results in agreement with Aguado *et al.*, 2007).

The evolutionary relationships of species that brood in gelatinous masses have been examined by the first time in the present morphological analyses. This brooding strategy appeared in some punctual epigamic species (*Amblyosyllis speciosa* and *Anoplosyllis edentula*) not closely related (Figs. 12-14), and therefore considered a parallelism. Viviparity appeared idependently in two terminals, *Dentatisyllis mortoni* and *Parexogone hebes* (Webster & Benedict, 1884), evolving from epigamic and schyzogamic modes, respectively. It could be reasonably interpreted as a convergent adaptation to their interstitial life. Several studies (Westheide, 1984, 1987) have examined the interstitial organisms finding that most of them converge in showing the same modifications in the reproductive patterns. The number of eggs is usually reduced and the parental cares are more frequent, being common to find viviparous species (Westheide, 1984, 1987).

Although the family was resolved as monophyletic in the reduced analysis (the second analysis carried out; Fig. 14), the relationships between syllids and the genus *Sphaerodoropsis* were not entirely resolved when including all the genera (first analysis, Fig. 12). The anatomy of the proventricle needs to be exhaustively studied and compared in both families in order to determine if it is a homologous structure or, rather, if there are other aspects that could be included as characters in a morphological analysis providing more information about its origin. Fauchald (1974) considered that the degree of development of the musculature in the proboscis varied within Sphaerodoridae, being useless to differentiate groups. However, such a well defined proventricle (quite similar to the syllid's proventricle) as it is in *S. anae*, has not been reported before in any other Sphaerodoridae taxa. Its finding suggests the necessity of studying it more carefully since it might prove useful for establishing important differences with other related families. The proventricle might have appeared independently in Sphaerodoridae and Syllidae as suggested by Aguado *et al*. (2007), yet we still need more morphological evidence to support this hypothesis.

We could not confirm that the synapomorphy of syllids is the presence of the proventricle, as it was previously suggested (Glasby, 1993). However, our results strongly support the hypotheses about the evolutionary role of the reproductive processes and their associated modifications in Syllidae (according with Garwood, 1991). The reproductive modes are the principal apomorphies that defined most of the monophyletic groups in this study (i.e. Exogoninae being divided in two clades

attending to the brooding system; Autolytinae defined by schyzogamy plus stolons that show dimorphism and regionalization; and Syllinae distinguished by schyzogamy plus stolons not differentiated). In addition, all these estrategies seem to be unique in polychaetes (San Martín, 2003). Nevertheless, the reproduction in syllids is surprisingly related to the role played by the proventricle. This organ has endocrine functions, apart from the digestive purposes, which are in common with the role that similar structures develop in other families (such as Sphaerodoridae and Nautiliniellidae). The proventricle in syllids plays an important role in the regulation of the endocrine activity during the reproductive cycle segregating hormones that inhibits a new stolonization process and stimulates the regeneration of the posterior part of the body (Franke, 1983, 1986; Heacox & Schroeder, 1982). When the levels of these hormones decrease, the stolonization starts again. Therefore, the presence of a specialized proventricle functioning as a gland might indicate the recovery of such an important structure as a synapomorphy of Syllidae. However, studies focused in the role of the proventricle during the reproductive processes have been only developed for some species of *Syllis* in the course of the stolonization process (Franke, 1983, 1986; Heacox & Schroeder, 1982).

The capacity of recovering lost structures such as notopodia, notoacicula and notochaeta during the reproductive phase might be another synapomorphy of Syllidae, especially since it does not occur in any other family of polychaetes. Thus, considering all these features together, namely, the proventricle being intimately linked with the reproduction in syllids as a main hormone producer, and the correlated appearance of special chaetae in the reproductive events, may be the evolutionary novelty that separated the group from the rest of polychaetes.

Although all the phylogenetic studies performed to date coincide in supporting equivalent monophyletic groups, the relationships between them do not coincide since each previous study comprised its own tree topology. For instance, Nygren & Sundberg (2003) reported Autolytinae as the sister group to Exogoninae, Syllinae and some Eusyllinae, while Aguado *et al*. (2007) found Exogoninae and Syllinae close to each other and Autolytinae more related with some members of Eusyllinae.

The morphological results presented herein illustrate a different combination whereby Syllinae and members of Eusyllinae are closer to each other, coinciding with the hypothesis in Nygren (1999), which was also exclusively grounded on

morphological data. The small incongruences possibly stem from the fact that different data were used, such as unequivalent number of taxa, in the election of terminals, or the nature of data *per se* (i.e. morphological or molecular). Evidently, a combined analysis including further evidences is still required in order to achieve a more conclusive hypothesis.

Aguado *et al.* (2007) showed that several taxa previously considered as Eusyllinae (*Nudisyllis*, *Odontosyllis Opisthodontha*, *Eusyllis* and several *Pionosyllis* species) formed a monophyletic group, even though it was somewhat poorly supported. These Eusyllinae genera appeared herein as a polytomy that also included *Palposyllis*, *Streptodonta*, *Paraehlersia* and Syllinae (Figs. 12, 14). Likely, if more morphological information and more sequences were provided these eusylline genera might constitute a supported monophyletic group for which the name Eusyllinae could remain valid if the group were redefined. Meanwhile, the current subfamily Eusyllinae shall be considered artificial and lacking any evolutionary meaning.

Autolytinae is defined by two apomorphies, namely, the reduction and fusion of ventral cirri to parapodia and presence of bayonet-shaped chaetae, despite being reversials in *Bollandia*, included within Autolytinae in the first analysis (Fig. 12). *Bollandia* was described with ventral cirri and with simple chaetae not described as bayonet-shaped (Glasby, 1994). However, the structures reported as ventral cirri could possibly be considered genital papillae since there is more than one pair per segment (Glasby, 2007, pers. com.). Likewise, the dorsal-most chaetae could be homologous with the bayonet-shaped ones given that they are similar in shape (Fig. 6K). If these interpretations are substantiated with further evidence elsewhere, both the inclusion of *Bollandia* within Autolytinae and the consideration of both features as the synapomorphies of Autolytinae (in agreement with Nygren, 1999, 2004 and Nygren & Sundberg, 2003) would all be corroborated.

Bollandia is an enigmatic genus for which other of its features could be interpreted differently. It was described as lacking antennae and with three pairs of "tentacular" cirri (Glasby, 1994) (Fig. 6M). However, it might otherwise have two pairs of "tentacular" cirri plus one pair that corresponds to the first chaetiger, the latter which is enlarged as it is typical in many Autolytinae. We also do not know whether the simple chaetae present in this genus are the result of a fusion process between the fang

and the blade or not, as it is the case in other syllids. Unfortunately, the interpretation of the special features of this taxon will remain speculative until further evidence is provided.

The articulation of appendages has been traditionally considered a diagnostic character to identify the Syllinae. However, *Haplosyllides* and *Alcyonosyllis,* are two genera which posses appendages that are either smooth or with a very weak articulation. These genera are raised as the sister group of the rest of Syllinae (Figs. 12, 13) implying that the presence of the smooth appendages could be the primitive condition within Syllinae. These two genera share with *Trypanoseta*, *Parahaplosyllis*, *Haplosyllis* and some species of *Syllis* the presence of simple chaetae derived from the common pattern of compound chaetae in Syllinae. Thus, the acquisition of these chaetae could be considered as a particular adaptation that appeared independently in different genera with symbiotic life styles (Glasby & Watson, Martin & Britayev, 1998; San Martín, 2003; Aguado *et al.*, submitted; Martin *et al.*, submitted).

Some genera such as *Karroonsyllis* and *Paraopisthosyllis*, not chiefly assigned to any of the traditional subfamilies to date, appear now within Syllinae (Fig. 12). However, their position within this clade shall remain uncertain until accounts about their reproductive mode are provided, since this is currently the only feature that defined the Syllinae.

Aguado *et al.* (2007) hypothesized that the pharyngeal tooth may have appeared in the common ancestor of all syllid genera with the exception of Clade I (*Astreptosyllis-Syllides* group), and then later reverting in particular terminals. However, the numerous possible combinations of chitinous structures (e.g. trepan, pharyngeal tooth and denticled arc) present in the same terminals, and the absence of any pharyngeal armature in other taxa, make difficult to delineate a possible hypothesis about the origin of these structures. Furthermore, the chitinous structures in Syllinae may be derived from a plastic ontogenetic process in some species. San Martin *et al.* (1997) described different specimens of the same population of *Haplosyllides floridana* Augener, 1924 with and without pharyngeal tooth. A similar situation has been described in some species of *Trypanosyllis*, which have a pharyngeal tooth plus a trepan when they are juveniles, whereas the adults only present a trepan (San Martín, 2003). We have also been able to examine several specimens of the genera *Trypanoseta* and *Haplosyllis*, finding a noticeable plasticity in the appearance of some pharyngeal

structures. Thus, the morphological information available to date is still insufficient to argue about the origin of pharyngeal structures in Syllidae.

In the first analysis, there was a lack of some resolution and the stability of the clades was low (Fig. 12). Terminal taxa showed a remarkable diversity in many features most of which allocated as homoplasies. In addition, there were many unknown characters and several 'inaplicables', a classical methodological problem, which often bears a very difficult solution (Pleijel, 1995). Some of these homoplasies relate with the shape, the spinulation and the length of chaetae, or with features that are traditionally applied for delineating the separation between subgroups of Syllidae, such as the articulation of appendages, the relative fusion of palps, or the presence of nuchal epaulettes. In the second analysis in which only the well-known genera were included, both the resolution and support values of the monophyletic groups were considerably higher, which arguably indicates that the missing and/or misleading information in the first analysis were likely the reason why there were ambiguities and low support values when all genera are considered.

Overall, these complex results underscore the need of more detailed comparative studies that incorporate as many as possible data coming from all facets of morphology, though specially anatomical and ontogenetic proxies. As other authors have previously suggested certain aspects of life diagram patterns could also be incorporated as additional characters (Fitzhugh, 1987). New material should nonetheless be studied fresh in order to be capable of codifying far more information that is obviously lost in the preserved material. However, further studies and DNA sequences from some key taxa, such as *Clavisyllis*, *Lamelisylis* and more sphaerodorids may also help to resolve these issues in the future.

CONCLUSIONS

The principal conclusions of all the analyses performed might be resumed in the following points:

- Autolytinae, Syllinae and Exogoninae are monophyletic groups, while Eusyllinae as currently delineated is paraphyletic.

- *Anoplosyllis, Astreptosyllis*, *Streptosyllis*, *Streptospinigera* and *Syllides* are a well-supported monophyletic group.
- *Amblyosyllis*, *Brachysyllis* and *Dioplosyllis* form another and well supported monophyletic group.
- Schizogamy derived from Epigamy appears twice in the family as different events.
- Exogoninae might be divided in two different groups with different brooding care systems: dorsal by notochaetae and ventral with eggs attached to nephridial pores.
- Some morphological features that had been traditionally used as diagnostic characters, such as the articulation of appendages and presence of nuchal eppaulettes, trepan or long and coiled pharynx, are homoplasies and they shoud not be used to differentiate groups, at least in exclusivity.

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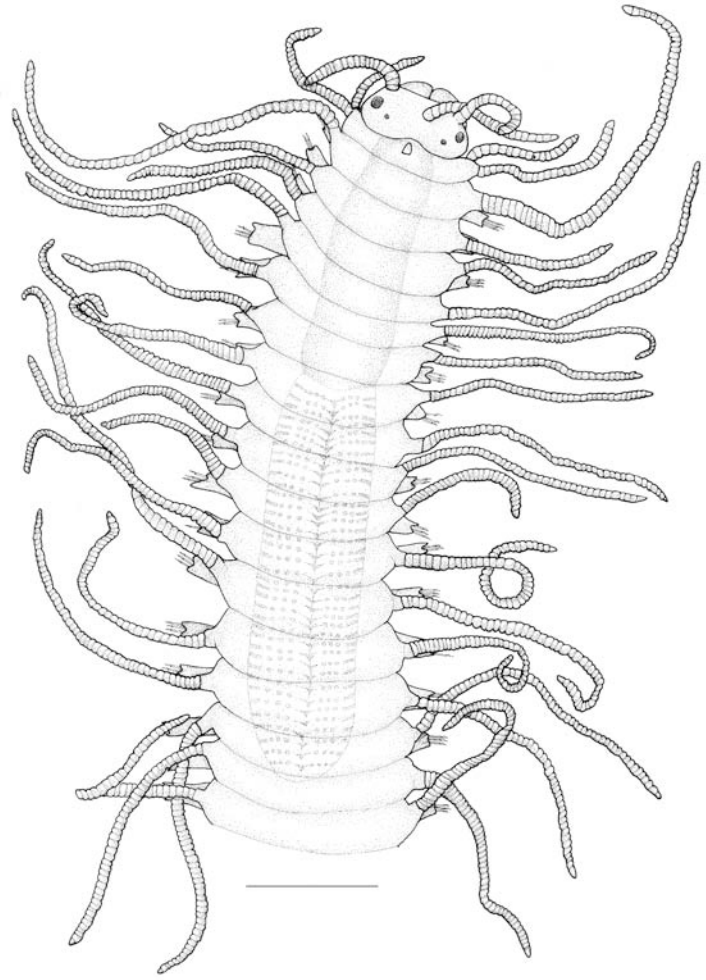
BLOQUE IV

PROPUESTA DE CLASIFICACIÓN



1. A proposal of classification of the family Syllidae Grube, 1850 with a new subfamily, keys of identification and diagnoses for all valid genera.

A proposal for the classification of the family Syllidae Grube, 1850 with a new subfamily, identification keys and diagnoses for all valid genera

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Abstract

A new classification for the Family Syllidae is proposed. This classification summarizes all the recent improvements on the systematics of syllids, being adjusted to our knowledge about natural groups from an evolutionary point of view. Three of the traditional subfamilies are maintained (Autolytinae, Syllinae and Exogoninae) since they have been proved to be monophyletic. One additional monophyletic group is proposed to be a new subfamily, the Anoplosyllinae. "Eusyllinae" is a term which lacks the rank of subfamily since it is paraphyletic. However, the name "eusyllinae" is maintained for grouping several genera until new results shed more light about their evolution. Finally, several genera whose phylogenetic relationships remain uncertain are shown within the "*incertae sedis*" until new results help us to clarify their relationships. Diagnoses of all recognized genera together with a catalogue of all valid species are also included.

Introduction

Classifications are needed to reduce the immense biodiversity into manageable groupings that allow us to sort, store and retrieve information, identify an unknown organism, infer unknown properties, and ultimately, to provide a baseline for comparative studies (Mayr & Bock, 2002).

However, there are many different systems of classification attending to different criteria. Traditionally, classifications of organisms have been made attending to similarities. For instance, in the family Syllidae the traditional classification was done taking into account several morphological features such as the articulation of the appendages, the fusion of palps, presence of nuchal epaulettes and presence of ventral cirri (see Table 1 in "Bloque III.2"). This classical organization of the group yielded

four subfamilies (Syllinae Grube, 1850; Exogoninae Langerhans, 1879; Eusyllinae Malaquin, 1893, and Autolytinae Langerhans, 1879) which was subsequently divided into numerous genera (Eusyllinae and Syllinae with the largest number). This clasification has been in use since the ending of the Nineteenth century, when it was established by Langerhans (1879) and Malaquin (1893), although several authors have suggested that it might be artificial, i.e that it does not reflect the natural evolution of the group (Fauchald, 1977; San Martín, 2003).

Natural classifications are those that correspond to the evolutionary history of a particular group of organisms and consist of their organization into so-called monophyletic units (Morrone, 2000). Mayr and Bock (2002) proposed several steps to be followed in order to perform a natural classification. They firstly considered that it was necessary to begin by reviewing the traditional taxonomic knowledge. Secondly, the partial studies summarized in a global database should be subjected to a genealogical analysis. Finally, the genealogical analysis results ought to be compared with the traditional classification, and when they showed that a taxon of a traditional classification had been placed in the wrong class, it should be shifted to its correct position. This system of classification ("Darwinian classification" as they named it) does not strongly modify the basic structure of the previous ordering system unless the phylogenetic analyses show that it was completely wrong (in evolutionary terms). In this context, the cladistic methodology emerged as a useful system that improves the traditional classifications providing them with an evolutionary meaning.

Equivalently, Kuntner and Agnarsson (2006) considered that the Linnean and the phylogenetic nomenclatural systems can coexist or be combined. A practical, nomenclatural approach that respects both tradition and novel advances in phylogenetic theory shall permit continue and accelerating biodiversity discovery, documentation, and research (Kuntner and Agnarsson, 2006). Following these suggestions, a new proposal of classification for the Syllidae that summarizes all the taxonomic and phylogenetic information available to date has been attempted herein. It is based on the traditional Linnean organization of the group but has been modified to be as far as possible in agreement with its phylogeny.

Between the large amounts of taxonomic studies considered in this study, some had a strong repercussion in the organization of Syllidae. For instance, Licher (1999) wrote a large and valuable revision of the genus *Syllis* clarifying many aspects of its difficult taxonomy. Nygren (2004) performed a phylogenetic revision of the subfamily

Autolytinae proposing a new classification for the group. San Martín (2005) studied the subfamily Exogoninae and summarized all the brooding modes present in the group. One year later, San Martín & Hutchings (2006) published a monography about Eusyllinae from Australia including the revised diagnosis of most of the genera ascribed to that group. The subfamily Syllinae has been revised by San Martín *et al.* (in press, submitted a) and Aguado & San Martín (in press) revised and re-described some of the most intriguing genera in Syllidae and clarified the interpretation of some morphological features in these taxa. Finally, the genus *Pionosyllis* was reorganized by San Martín *et al*. (submitted b) who performed a cladistic analysis including all the species belonging to that genus. As their results, the traditional diagnosis of *Pionosyllis* was emended and five new genera were proposed: *Synmerosyllis, Basidiosyllis, Westheidesyllis, Perkinsyllis,* and *Brevicirrosyllis*.

Dealing with the phylogeny of the group, Nygren (1999) and Aguado & San Martín (in prep.) performed phylogenetic analyses based on morphological information; and Nygren & Sundberg (2003) and Aguado *et al.* (2007) inferred phylogenetic hypotheses from molecular data. Additionally, Nygren (2004) combined both sources of information in an analysis focused only in Autolytinae. The strict consensus topologies of the phylogenetic analyses that included a higher number of taxa (Aguado *et al.*, 2007 and Aguado & San Martín, in prep.) are shown in the Fig. 1. However, both analyses are not equivalent since the terminals included were not exactly the same. In the morphological analysis of Aguado & San Martín (in prep.) all the recognized genera until date were included but only one species represented each of them; in contrast, in the analysis of Aguado *et al.* (2007) fewer genera were included but represented by several species.

We address a new classification based on the congruency of the previous taxonomic and phylogenetic studies as a transitory tool, useful until our plan of a complete combined analysis including both sources of data (molecular and morphological) is performed. A dichotomic key reaching down to genera and an extensive catalogue including all the valid species of each genus are also included.

Materials and methods

All the information used for this study was acquired from literature sources. The classification for Autolytinae and diagnoses of genera proposed by Nygren (2004),

Licher (1999); San Martín (2005), San Martín & Hutchings (2006), San Martín *et al.* (in press, submitted a, b) and Aguado & San Martín (in press) have been incorporated as well. Apomorphies of the subfamilies have been included from the analysis of Aguado & San Martín (in prep.). Two more genera that are in due description elsewhere are also added. All the material, the institutions involved, as well as all the methodologies and their particularities are explained in extension in their corresponding publications.

Results

The Syllidae currently has 73 valid genera and a total of 721 species (Table 1). 90 species have been recognized within Autolytinae, 216 species within Exogoninae, 251 species within Syllinae, and 38 species within Anoplosyllinae n. subfam. Additionaly, 90 species have been considered to momentarily belong to the artificial group "Eusyllinae", and 36 more species are still considered *incertae sedis*.

Taxonomic rank	**Subfamily**	**Subfamily**	**Subfamily**	**Subfamily**	-	-
Name of group	**Autolytinae**	**Exogoninae**	**Syllinae**	**Anoplosyllinae**	**"eusyllinae"**	***Incertae sedis***
Included genera	*Bollandia* (1) *Epigamia* (9) *Imajimaea* (4) *Levidorum* (4) *Myrianida* (29) *Pachyprocerastea* (1) *Paraproceraea* (1) *Paraprocerastea* (1) *Planicirrata* (1) *Proceraea* (26) *Procerastea* (5) *Virchowia* (6)	*Brania* (6) *Cicese* (1) *Erinaceusyllis* (26) *Exogone* (42) Genus 1 (2) *Parapionosyllis* (17) *Parexogone* (30) *Prosphaerosyllis* (26) *Salvatoria* (32) *Sphaerosyllis* (34)	*Alcyonosyllis* (5) *Branchiosyllis* (13) *Dentatisyllis* (7) *Eurysyllis* (5) Genus 2 (6) *Haplosyllides* (3) *Haplosyllis* (17) *Inermosyllis* (4) *Karroonsyllis* (1) *Megasyllis* (4) *Nuchalosyllis* (1) *Opisthosyllis* (16) *Parahaplosyllis* (1) *Paraopisthosyllis* (4) *Parasphaerosyllis* (4) *Plakosyllis* (2) *Rhopalosyllis* (1) *Syllis* (134) *Tetrapalpia* (1) *Trypanoseta* (2) *Trypanosyllis* (17) *Xenosyllis* (3)	*Anoplosyllis* (2) *Streptospinigera* (2) *Astreptosyllis* (2) *Streptosyllis* (13) *Syllides* (19)	*Basidiosyllis* (3) *Brevicirrosyllis* (5) *Eusyllis* (9) *Nudisyllis* (4) *Odontosyllis* (38) *Opisthodonta* (12) *Palposyllis* (1) *Paraehelersia* (4) *Pionosyllis* (7) *Streptodonta* (1) *Synmerosyllis* (3) *Westheidesyllis* (3)	*Amblyosyllis* (10) *Anguillosyllis* (3) *Brachysyllis* (3) *Clavisyllis* (1) *Dioplosyllis* (2) *Lamellisyllis* (1) *Miscellania* (1) *Murrindisyllis* (1) *Neopetitia* (3) *Nooralia* (1) *Psammosyllis* (3) *Perkinsyllis* (7)

Table 1. All the current valid genera of the Family Syllidae organized into four subfamilias and two groups without taxonomic rank. The number of valid species on each genus appears between brackets.

Discussion

In agreement with Aguado *et al.* (2007), Aguado & San Martín (in prep.) and previous authors (Nygren, 1999, 2004; Nygren & Sundberg, 2003) we have maintained the groups Autolytinae, Syllinae and Exogoninae as subfamilies because they came out as monophyletic groups in all these different phylogenetic analyses (Fig. 1).

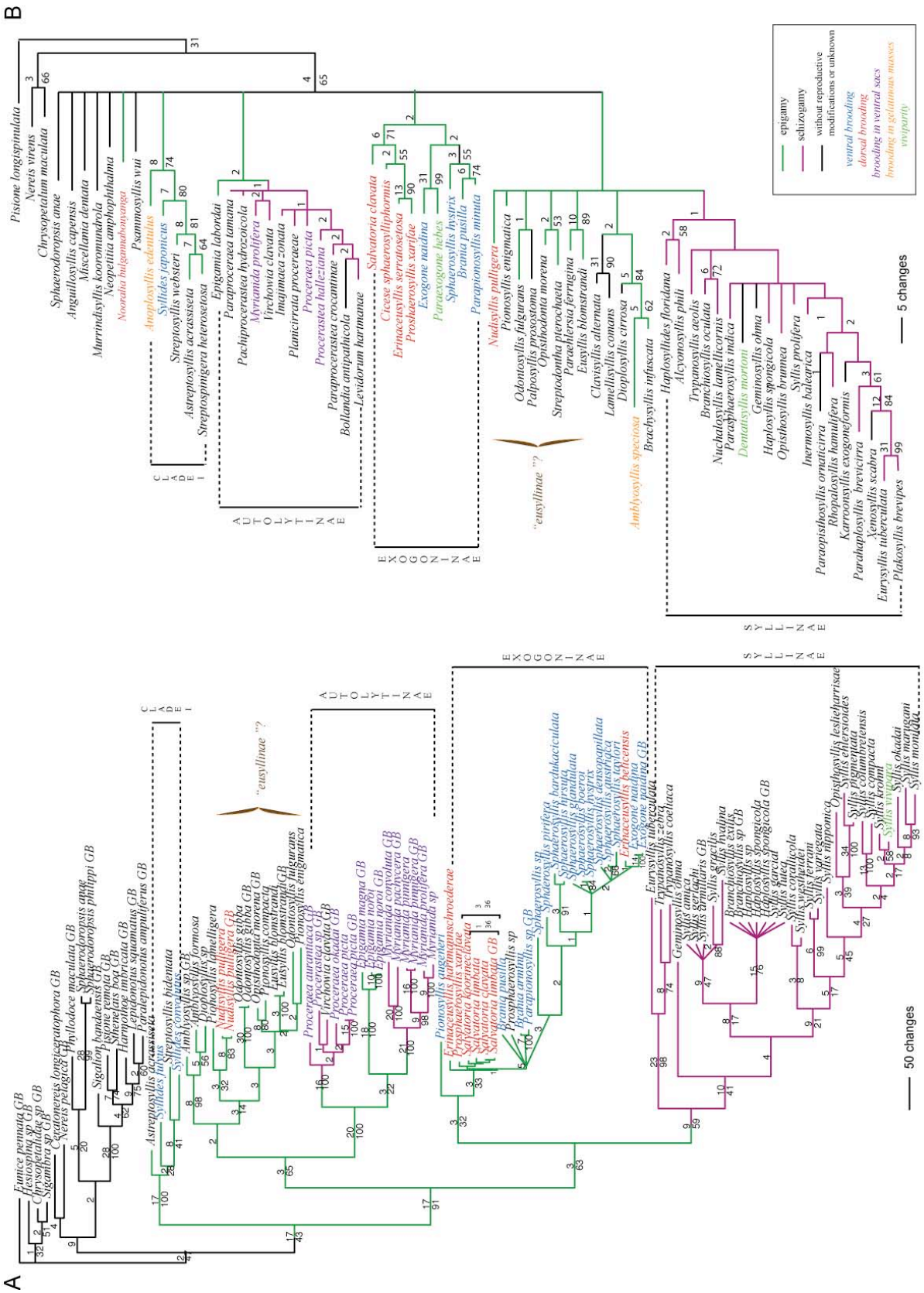

Figure 1. A. Strict consensus obtained from the combined molecular analysis of Aguado *et al.* (2007); B. Strict consensus obtained from the morphological analysis including all the valid genera until date of Syllidae by Aguado & San Martín (in prep.).

An additional well supported monophyletic group was found in both analyses; the Clade I, which might receive a taxonomic category in the classification (Figs. 1A, B). Several authors have dealt with the challenge of translating the results of a phylogenetic analysis into a natural classification (Wiley, 1981 and Forey, 1992 in Morrone, 2002). They proposed the principle of "subordination" to be applied, which indicates that each monophyletic group might receive the same category of its sister group. Following this principle and only considering the topology of the strict consensus by Aguado *et al.*, (2007), which is the most resolved, there might be three possible options for classifying correctly the Clade I. The first one might consist in considering it as a different Family and reorganize Syllidae without this group but including Autolytinae, Syllinae, Exogoninae as subfamilies and the rest of the misplaced genera. However, Syllidae, although supported by low values (especially the symmetric resampling values) came out as a monophyletic group, hence dividing it would be not properly justified.

The second option may maintain the Syllidae as a family, later divided into two subfamilies (Clade I and the rest of syllids). This second option may need to change the classical category of Exogoninae, Autolytinae and Syllinae translating them from subfamilies to tribes, subsequently changing all the categories within them (e.g. tribes within Autolytinae proposed by Nygren, 2004). The third solution might pass by maintaining Syllidae as a Family and Autolytinae, Exogoninae and Syllinae as subfamilies grouped together with some misplaced genera in a "supersubfamily". Then, its sister group, the Clade I, might receive the same category of "supersubfamily". However, category of "supersubfamily" has not been proposed before as valid in the Linnean classification. Any of these three possibilities seem to have strong implications in the final classification being necessary to find more support from other sources of data (morphological analyses) to choose one of them.

On the other hand, results of Aguado & San Martín (in prep.) also support the Clade I, which included more genera, but the relationships with the rest of the monophyletic groups remained uncertain. Considering the strict consensus (Fig. 1B), four groups are monophyletic, being three of them subfamilies in the traditional classification. Considering both results, the information in which they coincided was the less resolved option (in agreement with the morphological results), which yielded four monophyletic groups. The classification of Syllidae, in our opinion, should illustrate its phylogeny as simply as possible yet always in agreement with evidences available. This classification

can change into a more e complex system when new findings from different sources are introduced.

Since a more comprehensive analysis including more molecular and morphological information about more taxa is already in course, so far at the current stages of knowledge, the results supported by all the analyses showed that four groups are monophyletic, three of them correspond to three classical subfamilies, and hence the fourth might receive same category. Therefore, Clade I might be transitorily given the category of subfamily. We propose the name Anoplosyllinae to indicate that the subfamily encloses the clade including *Anoplosyllis* and *Streptospinigera* (Fig. 1B).

In addition, the classical subfamily Eusyllinae was found to be paraphyletic. However, Aguado *et al.* (2007) and Aguado & San Martín (in prep.) suggested that a group including some genera traditionally assigned to Eusyllinae may be monophyletic (Figs. 1A, B), and therefore, the name Eusyllinae might be valid after the reorganization of the included genera. Attending to this hypothesis we have maintained the name "eusyllinae" without a taxonomic category, to continue in use until the possible monophyly of these genera is resolved. We incorporated the genera suggested by the results of Aguado *et al.* (2007) and Aguado & San Martín (in prep.) within this possible group (Figs. 1A, B; Table 1). Finally, there are several genera whose evolutionary relationships are still doubtful and therefore, they are included in another group without a phylogenetic meaning ("*incertae sedis*" genera; Fig. 1B; Table 1).

The genera proposed by San Martín *et al.* (submitted b) in which the traditional "*Pionosyllis*" was divided were not incorporated in the most recent phylogenetic analyses (Aguado *et al*., 2007; Aguado & San Martín, in prep.) because all these analyses were being performed simultaneously. However, the five additional genera proposed by these authors have been included herein although we don't have complete phylogenetic evidence about their relationships. The molecular analysis of Aguado *et al.* (2007) included representatives of two of these additional groups: *Synmerosyllis* (represented by *P. lamelligera*) and *Perkinsyllis* (represented by *P. augeneri*) (Fig. 1A). *Synmerosyllis* was placed in the monophyletic group proposed here to be labelled as "eusyllinae", whereas *Perkinsyllis* appeared as the sister group of Exogoninae (Fig. 1A). Consequently, *Perkinsyllis* is included herein within the "*incertae sedis*" group, while *Synmerosyllis* is grouped within the "eusyllinae" group. The remaining three genera (*Westheidesyllis*, *Brevicirrosyllis* and *Basidiosyllis*) were proposed to be evolutionary related to the emended *Pionosyllis* and *Synmerosyllis* by San Martín *et al*. (submitted b).

Following these authors, they are grouped in this study within "eusyllinae" while more inclusive phylogenetic analyses reveal their relationships.

The genera *Amblyosyllis*, *Brachysyllis* and *Dioplosyllis* were also found as a well supported monophyletic group by both phylogenetic analyses (Figs. 1A, B). They are included herein within the "*incertae sedis*" group because of their possible relationships with the puzzling *Clavisyllis* and *Lamellisyllis* are not clarified. All these genera (*Amblyosyllis*, *Brachysyllis*, *Dioplosyllis*, *Clavisyllis* and *Lamelisyllis*) may constitute an additional group but the three former need an internal reorganization (several species might be synonymies) and the two latter are still quite unknown (Aguado & San Martín, in press).

The species proposed by Licher (1999) to pertain to the genera "*Typosyllis*" and *Syllis* have been considered but all of them belonging to the genus *Syllis*, since we do not accept "*Typosyllis*" as others authors have previously done (San Martín, 1984, 2003).

Proposal of new classification for Syllidae

Family Syllidae Grube, 1850

Key to genera of subfamilies and groups

1.- Ventral cirri absent……Subfamily Autolytinae

.- Ventral cirri present……2

2.- Pharynx unarmed. Anterior appendages smooth, other dorsal cirri pseudoarticulated or smooth.……..……..Subfamily Anoplosyllinae n. subfam.

.- Pharynx provided of middorsal tooth or trepan, or both (few exceptions unarmed). Dorsal cirri articulated anteriorly and smooth from midbody, or all smooth or all articulated……..…….3

3.- Antennae, tentacular cirri and dorsal cirri articulated. Reproduction by schizogamy…….…..Subfamily Syllinae (most genera)

.- These appendages smooth…….4

4.- Only thick, simple chaetae. Reproduction by schizogamy…Subfamily Syllinae (few genera)

.- Chaetae compound (sometimes few thick simple chaetae). Reproduction by epigamy (unkown in some genera)……...5

5.- Antennae, tentacular and dorsal cirri short or medium size. Dorsal or ventral brooding. Palps fused all along their length or approximately to half length ……..……...Subfamily Exogoninae

.- Antennae, tentacular and dorsal cirri long. Except for few genera, no brooding. Palps free or basally fused.……. “Eusyllinae”

Those other with other characters, see “*Incertae sedis*”

Subfamily ***Anoplosyllinae*** n. subfam.

Diagnosis. Body cylindrical, size from small to minute. Palps basally fused, without medial scar. Three antennae, usually long, extending beyond palps. Four lensed eyes and sometimes two anterior eyespots. Two pairs of tentacular cirri. Nuchal organs consist in two dorsolateral, densely ciliated grooves between prostomium and peristomium. Pharynx straight, relatively short, without any armature. Antennae, tentacular cirri and anterior dorsal cirri smooth; remaining dorsal cirri smooth or articulated, with articles strongly marked by constrictions. Reproduction by epigamy; one species is reported to brood eggs.

Apomorphies. The subfamily is defined by one uncontradicted apomorphy: ventral cirri medially inserted; and two apomorphies with reversials and homoplasy: presence of granules on the dorsum of peristomium (reverting in *Astreptosyllis* and *Streptospinigera*) and the absence of pharyngeal tooth (in common with several groups, such as Autolytinae, *Murrindisyllis*, *Nooralia*, *Odontosyllis*, *Anguillosyllis*, *Anoplosyllis*, *Bollandia*, *Amblyosyllis*, *Xenosyllis*, *Inermosyllis* and *Trypanosyllis*).

Key to species

1.- Aciculae of some anterior parapodia with inflated tips…….. *Streptosyllis*

.- Aciculae without inflated tips …… 2

2.- Dorsal cirri all smooth, more or less club-shaped …… *Anoplosyllis*

.- Dorsal cirri from chaetiger 3 distinctly articulated …… 3

3.- Two kinds of chaetae; some anterior parapodia with thick shafts and short, enlarged blades…….…… *Astreptosyllis*

.- Single kind of chaetae…… 4

4.- Dorsal simple chaetae with distinct, longitudinally striated, distal hood. Compound chaetae unidentate. Ventral cirri of posterior parapodia distinctly elongated……...… *Streptospinigera*

.- Dorsal simple chaetae without hood, or if present, small and not striated. Compound chaetae bidentate. Ventral cirri not elongated……. *Syllides*

Genus ***Anoplosyllis*** Claparède, 1868

Anoplosyllis Claparède, 1868: 214.

Type species. *Anoplosyllis edentula* Claparède, 1868.

Diagnosis. Body small, (< 5 mm in length), with up to 30 chaetigers. Prostomium rectangular, similar width to anterior segments, with 2 pairs of eyes and 2 anterior eyespots. Three antennae. Palps small, fused basally, without median furrow. Nuchal organs as 2 ciliated grooves between prostomium and peristomium. Two pairs of tentacular cirri. Antennae, tentacular and dorsal cirri smooth, club-shaped, tapered basally, longer than parapodial lobes. Compound chaetae heterogomph, blades slender, elongate, unidentate or indistinctly bidentate. Dorsal and ventral simple chaetae present on some parapodia. Pharynx shorter than proventricle, unarmed. Proventricle large, almost as wide as body. Some species brood eggs in gelatinous masses.

Species and distribution. The genus is cosmopolitan. *Anoplosyllis edentula* Claparède, 1868; *Anoplosyllis sexoculata* (Hartmann-Schröder, 1962).

Bibliography. Cognetti-Varriale (1971); San Martín (2003); San Martín & Hutchings (2006).

Genus ***Astreptosyllis*** Kudenov & Dorsey, 1982

Astreptosyllis Kudenov & Dorsey, 1982: 575.

Type species: *Astreptosyllis acrassiseta* Kudenov & Dorsey, 1982.

Diagnosis. Body of meiofaunal size. Prostomium with 2 pairs of eyes and 3 antennae. Palps fused basally, small but visible dorsally without median furrow. Nuchal organs as 2 ciliated grooves between prostomium and peristomium. Two pairs of tentacular cirri. Antennae, tentacular cirri and dorsal cirri of 2 anterior chaetigers not articulated, club-shaped, slender basally and distally slightly inflated, longer than body width; from chaetiger 3 onwards, dorsal cirri articulated, articles elongated to pyriform, with dark, glandular inclusions. Parapodial lobes subrectangular on anterior parapodia, conical and elongated from midbody; ventral cirri short and broad on anterior parapodia, posteriorly becoming more elongated, digitiform. Compound chaetae heterogomph or hemigomph falcigers. Dorsal simple chaetae thick, provided with distal, longitudinally striated hood. Ventral simple chaetae sometimes present on far posterior parapodia, but usually

lacking. Pharynx unarmed, with distal crown of soft papillae. Pygidium with 2 anal cirri.

Remarks. Details on reproduction unknown, it might reproduce by epigamy as other genera in Anoplosyllinae.

Species and distribution. The genus is only known from Australia. *Astreptosyllis acrassiseta* Kudenov & Dorsey, 1982; *Astreptosyllis similiseta* Hartmann-Schröder, 1986.

Bibliography. Kudenov & Dorsey (1982); San Martín & Hutchings (2006).

Genus ***Streptosyllis*** Webster & Benedict, 1884

Streptosyllis Webster & Benedict, 1884: 711.

Type species. *Streptosyllis arenae* Webster & Benedict, 1884, by monotypy.

Diagnosis. Body small (< 5 mm in length), with up to about 40 chaetigers, usually 20-30. Prostomium with 4 eyes and 2 anterior eyespots. Three antennae. Palps fused at bases, without median furrow, sometimes terminating with 2 papillae, occasionally reduced. Nuchal organs as 2 ciliated grooves between prostomium and peristomium. Dorsal cirri usually smooth or indistinctly articulated, club-shaped to elongated, sometimes with glandular inclusions. Ventral cirri digitiform, sometimes distinctly longer than parapodial lobes and pseudoarticulated, arising from middle of parapodia. Compound chaetae, homogomph to hemigomph, blades falcigerous or, exceptionally, some spiniger-like chaetae. Dorsal simple chaetae present usually from chaetiger 1. Ventral simple chaetae absent. Aciculae from some anterior parapodia distinctly enlarged. Pharynx unarmed, provided with crown of soft papillae. Proventricle with poorly defined muscle cell rows. Reproduction by epigamy.

Species and distribution. The genus is cosmopolitan. *Streptosyllis aequiseta* Hartmann-Schröder, 1981; *Streptosyllis arenae* Webster & Benedict, 1884; *Streptosyllis biarticulata* Hartmann-Schröder, 1991; *Streptosyllis bidentata* Southern, 1914; *Streptosyllis campoyi* Brito, Núñez & San Martín, 2000; *Streptosyllis cryptopalpa* Hartmann-Schröder, 1960; *Streptosyllis latipalpa* Banse, 1968; *Streptosyllis magnapalpa* Hartmann-Schröder, 1981; *Streptosyllis reducta* Hartmann-Schröder, 1960; *Streptosyllis templadoi* San Martín, 1984; *Streptosyllis varians* Webster & Benedict, 1887; *Streptosyllis verrilli* (Moore, 1908); *Streptosyllis websteri* Southern, 1914;

Bibliography. Garwood (1982); Sardá & San Martín (1992); Brito, Núñez & San Martín (2000).

Genus ***Streptospinigera*** Kudenov, 1983

Streptospinigera Kudenov, 1983: 84-85.

Type-species. *Streptospinigera heteroseta* Kudenov, 1983.

Diagnosis. Body small, short, with relatively few segments. Ptrostomium with 2 pairs of eyes and a pair on eyespots, 3 antennae and 2 pals. Palps fused basally, distally rounded, blunt. Two pairs of tentacular cirri. Antennae, tentacular cirri, and anterior dorsal cirri smooth, club-shaped, smooth and elongated on midbody and abruptly becoming strongly articulated on posterior parapodia. Parapodial lobes distally beak-shaped to truncate, anterior ones twice as thick as the rest. Ventral cirri digitiform, not extending beyond parapodial lobes. Compound chaetae with falcigers and spiniger-like blades on same parapodium. Blades of falcigers thick on anterior parapodia, abruptly becoming slender thereafter. Spinger-like chaetae present from midbody backwards, with slender shafts. Dorsal simple chaetae present from anterior parapodia, distally falcate, thick on anterior parapodia, abruptly becoming slender, capillary. Pygidium with 1 midventral and 2 dorsolateral anal cirri. Pharynx unarmed.

Species and distribution. Only two species known from Gulf of México and Japan. *Streptospinigera heteroseta* Kudenov, 1983; *Streptospinigera alternocirra* Ohwada, 1988.

Bibliography. Kudenov (1983).

Genus ***Syllides*** Örsted, 1845

Syllides Örsted, 1845a: 408.

Type-species: *Syllides longocirrata* Örsted, 1845.

Diagnosis. Body small, short, with relatively few segments. Prostomium with 4 eyes, typically pair of anterior eyespots. Three antennae. Palps fused basally, without median furrow, sometimes ending in small papilla. Two pairs of tentacular cirri. Nuchal organs as 2 ciliated grooves between prostomium and peristomium. Antennae, tentacular cirri, and dorsal cirri of chaetigers 1 and 2 not articulated, club-shaped to fusiform; dorsal cirri from chaetiger 3 onwards, distinctly articulated, with glandular inclusions on some articles. Ventral cirri digitiform. Compound chaetae heterogomph with blades slender, usually bidentate. Dorsal simple chaetae from anterior segments, usually from chaetiger

1. Ventral simple chaetae present in some species. Pharynx unarmed, with crown of soft papillae. Reproduction by epigamy, some species brood eggs ventrally (Heacox & Schroeder, 1978).

Species and distribution. The genus is cosmopolitan. *Syllides articulosus* Ehlers, 1879, *Syllides bansei* Perkins, 1981; *Syllides benedicti* Banse, 1971; *Syllides caribica* Licher, 1996; *Syllides convolutus* Webster & Benedict, 1884; *Syllides eburneus* Riser, 1997; *Syllides edentatus* Westheide, 1974; *Syllides floridanus* Perkins, 1981; *Syllides fulvus* (Marion & Bobretzky, 1875); *Syllides gomezi* San Martín, 1990; *Syllides japonicus* Imajima, 1966; *Syllides longocirrata* Örsted, 1845; *Syllides minutes* Blake & Walton, 1977; *Sylides papillosus* Hartmann-Schröder, 1960; *Syllides pumilus* Hartmann-Schröder, 1983; *Syllides reishi* Dorsey, 1978; *Syllides setosus* Verrill, 1882; *Syllides spinosus* Hartmann-Schröder, 1979; *Syllides tam* San Martín & Hutchings, 2006.

Bibliography. Banse (1972); Heacox & Schroeder, 1978; San Martín (2003); San Martín & Hutchings (2006).

Subfamily **Autolytinae** Langerhans, 1879

Diagnosis. Body cylindrical, size from medium to large. Palps fused, usually ventrally folded. Three antennae, usually long, extending beyond palps (one genus without antennae). Four lensed eyes and sometimes two anterior eyespots. Two pairs of tentacular cirri, typically long and slender. Two nuchal epaulettes (indistinct or absent in some genera). Ventral cirri absent. Dorsal simple chaetae often bayonet-shaped. Pharynx slender, usually long and convoluted. Middorsal tooth absent; trepan present (two genus unarmed). Dorsal cirri smooth, sometimes with a distinct cirrophore. Reproduction by schizogamy (one genus by epigamy).

Remarks. In agreement with Aguado & San Martín (in prep.) (Fig. 1B), we have considered that *Bollandia* might be included in this subfamily.

Apomorphies. Reduction of ventral cirri and dorsal simple chaetae bayonet shaped. Both apomorphies are reversials in *Bollandia*.

Key to genera (modificated from Nygren, 2004)

1.- Pharynx unarmed. Only two chaetae per parapodium, one slender and other thicker, both simple. Parasitic on black corals……...*Bollandia*

.- Pharynx with trepan. Different chaetae. Associated to other marine invertebrates or free living…….....2

2.- Appendages absent……..……..*Levidorum*

.- Appendages present, at least anteriorly……..……..3

3.- Antennae, tentacular cirri and dorsal cirri of chaetiger 1 present; remaing appendages absent……*Procerastea*

.- Dorsal cirri on all chaetigers……4

4.- Large, clavate, dorsal cirri alternate with much smaller, cylindrical or clavate cirri. Nuchal epaulettes on especial outgrowths……..……..*Virchowia*

.- Appendages and nuchal epaulettes different……5

5.- Dorsal cirri from chaetiger 2 short, small, egg-shaped. Only simple chaetae…….……..*Paraprocerastea*

.- Dorsal cirri different. Usually compound chaetae (with some exceptions)……..6

6.- Dorsal cirri small, flattened. Reproduction by anterior scissiparity……*Planicirrata*

.- Dorsal cirri cylindrical or, if flattened, long and wide……...7

7.- Nuchal epaulettes short, reaching to half of tentacular segment. All cirrostyles equal, short, cylindrical. Parapodia with compound, simple thick chaetae and bayonet chaeta. Reproduction by anterior scissiparity……..……...*Pachyprocerastea*

.- Different characters……..8

8.- Colour pattern as brown to black transverse intersegmental bands. Cirrostyles egg-shaped. Reproduction by anterior scissiparity…….……*Imajimaea*

.- Different characters……...9

9.- Nuchal epaulettes extending to chaetiger 3. More than 65 teeth on trepan…….....*Paraproceraea*

.- Nuchal epaulettes shorter. Less than 65 teeth on trepan……10

10.- Reproduction by epigamy……*Epigamia*

.- Reproduction by schizogamy……..11

11.- Trepan in two rows. Bayonet chaetae distally thick (one exception). Reproduction by anterior scissiparity…….…….....*Proceraea*

.- Trepan in a single row. Bayonet chaetae distally slender. Reproduction by gemmiparity…….*Myrianida*

Genus ***Bollandia*** Glasby, 1994

Bollandia Glasby, 1994: 616.

Type-species. *Bollandia antipathicola* Glasby, 1994

Diagnosis (modified from Glasby, 1994)**.** Body of small size, with numerous chaetigers, higly arched dorsally, flat-concave ventrally. Dorsum, parapodia and cirri covered by clumps of cilia. Prostomium small with two pairs of eyes. First two segments

cephalized, fused together and with peristomium. Antennae and palps absent, nuchal organs not externally exposed. Three pairs of appendages on anterior end, most probably representing one pair of peristomial cirri and two pairs of tentacular cirri. All the appendages not articulated, conical with tapering end. Two simple neurochaeta per parapodium, one sigmoid and another distally bent. Sinuous, unarmed pharynx, and barrel-shaped proventriculus. Two annal cirri.

Species and distribution. Type-species, parasitic on black corals from Japan.

Bibliography. Glasby (1994); Aguado & San Martín (in prep.).

Genus ***Epigamia*** Nygren, 2004

Epigamia Nygren, 2004: 163.

Type-species. *Autolytus noroi* Imajima & Hartman, 1964

Diagnosis. Body of small size, with numerous chaetigers, cylindrical, ventrally flattened. Two rows of cilia per segment. Prostomium with 4 eyes, sometimes 2 eyespots. Palps fused at base or completely fused. Nuchal epaulettes from chaetiger 1 to end of chaetiger 6. Three antennae, median antenna inserted medially on prostomium; lateral antennae on anterior margin. Two pairs of tentacular cirri. Dorsal cirri commonly alternating in length; cirrophores equal, shorter or equal in length to parapodial lobes. All appendages cylindrical, with one exception, in which dorsal cirri are flattened on some parapodia. Parapodial lobes large, more or less rounded. Dorsal bayonet chaetae, subdistally denticulated, and compound chaetae with bidentate blades. Pharynx with single to multiple sinuations. Trepan with various types of denticulation, in 1-3 rings. Basal ring present; infradentale spines absent or present. Pygidium with 2 anal cirri, without median papilla. Reproduction by epigamy.

Species and distribution. Nine species known of this genus and one questionable species. The genus is distributed by polar, subpolar and temperate seas. *Epigamia alexandri* (Malmgren, 1867); *Epigamia alternata* (Imajima & Hartman, 1964); *Epigamia charcoti* (Gravier, 1906); *Epigamia labordai* (San Martín & López, 2002); *Epigamia macrophthalma* (Marenzeller, 1875); *Epigamia magna* (Berkeley, 1923); *Epigamia noroi* (Imajima & Hartman, 1964); *Epigamia planipalpa* (Chamberlin, 1919); *Epigamia usaensis* (Imajima, 1966); *Epigamia* (?) *profunda* San Martín, 2004.

Bibliography. Gidholm (1966); Hamond (1974); Nygren (2004).

Genus ***Imajimaea*** Nygren, 2004

Imajimaea Nygren, 2004: 105.

Type-species. *Autolytus japonensis* Imajima & Hartman, 1964

Diagnosis. Body of medium size, with numerous chaetigers, cylindrical, ventrally flattened. Colour pattern as transverse brown/black intersegmental bands (unknown in one species). Ciliation unkown. Prostomium with 4 eyes. Palps fused. Nuchal epaulettes from end of tentacular segment to end of chaetiger 1. Three antennae, median antenna inserted medially on prostomium, lateral antennae on anterior margin. Two pairs of tentacular cirri. Dorsal cirri from chaetiger 3 of equal length; cirrophores present on tentacular cirri and first dorsal cirri, otherwise absent, Anterior appendages cylindrical or flaskshaped, dorsal cirri cylindrical or ovoid to egg shaped. Parapodial lobes rounded to rounded conical, small or medium size. Simple chaetae present on chaetiger 1-4, in all chaetigers, or absent; simple chaetae uni- or bidentate, with small distal tooth. Dorsal bayonet chaetae, subdistally denticulated. Compound chaetae with bidentate blades. Pharynx with single to multiple sinuation anterior and lateral to proventricle. Trepan arranged in 1 ring, with equal teeth, or with 2 large lateral teeth in combination with irregularly sized and arranged teeth. Basal ring present; infradentale spines absent. Pygidium with 2 anal cirri, without median papilla. Reproduction by schizogamy by anterior scissiparity.

Species and distribution. Four known species; one from N Spain, two from Japan, and one from Kuwait. *Imajimaea draculai* (San Martín & López, 2002); *Imajimaea japonensis* (Imajima & Hartman, 1964); *Imajimaea tsugara* (Imajima, 1966); *Imajimaea zonata* (Mohammad, 1973).

Bibliography. Nygren (2004).

Genus ***Levidorum*** Hartman, 1967

Levidorum Hartman, 1967: 84.

Type-species. *Levidorum scotiarum* Hartman, 1967

Diagnosis. Body of small to medium size, with numerous chaetigers, cylindrical, ventrally flattened. Ciliation absent on one species, unknown on others. Prostomium without or with 4 eyes, with a dorsal, transverse furrow on some species. Palps fused, reduced or absent. Nuchal epaulettes absent. Without antennae, tentacular cirri and dorsal cirri. Parapodial lobes rounded to conical, very small. All chaetae simple, knob-like. Bayonet chaetae absent. Pharynx with single sinuation anterior and lateral to

proventricle. Trepan arranged in 1 ring, with 5 equal teeth. Basal ring present; infradentale spines absent. Reproduction by schizogamy by anterior scissiparity.

Species and distribution. Only four species known; Mediterranean and Gulf of México. *Levidodum hartmanae* Perkins, 1987; *Levidorum pettiboneae* Perkins, 1987; *Levidorum pori* (Ben-Eliahu, 1977); *Levidorum scotiarum* Hartman, 1967.

Bibliography. Perkins (1987); San Martín (2003); Nygren (2004).

Genus ***Myrianida*** Milne Edwards 1845

Myrianida Milne Edwards, 1845: 180

Scolopendra Slabber, 1781

Podonereis Balinville, 1818

Autolytus Grube, 1850

Diploceraea Grube, 1850

Sacconereis J. Muller, 1853

Crithida Gosse, 1855

Sylline Grube, 1860

Monocerina Costa, 1861

Eucerastes Quatrefages, 1865

Autolytides Malaquin, 1893

Type-species. *Myrianida fasciata* Milne Edwards, 1845

Diagnosis. Body of small to large size, with numerous chaetigers, cylindrical, ventrally flattened. One or two rows of cilia per segment. Prostomium with 4 eyes, sometimes 2 eyespots. Palps fused at base or completely fused. Nuchal epaulettes extended over several segments, from the end of persitomium 1 to end of chaetiger 12. Three antennae, median antenna inserted medially on prostomium; lateral antennae on anterior margin. Two pairs of tentacular cirri. Cirri, cirrophores, cyrrostyles may be equal in length or altenating. Appendages cylindrical, thick and swollen, slightly flattened or flattened. Parapodial lobes medium in size, rounded, with dorsal part prolonged in some species. Dorsal bayonet chaetae thin, subdistally denticulated, and compound chaetae with bidentate blades. Pharynx with single to multiple sinuations. Trepan with various types of denticulation, in 1 ring. Basal ring absent or present; infradentale spines absent or present. Pygidium with 2 anal cirri, without median papilla. Reproduction by gemmiparous schizogamy.

Species and distribution. Numerous species. The genus is cosmopolitan. *Myrianida antondohrni* Çinar & Gambi, 2005; *Myrianida arborea* (Westheide, 1974); *Myrianida australiensis* (Hartmann-Schróder, 1982); *Myrianida brachycephala* (Marenzeller, 1874); *Myrianida brevicirrata* (Winternitz, 1936); *Myrianida brevipes* (Hartmann-Schröder, 1959); *Myrianida cognettii* Çinar & Gambi, 2005; *Myrianida convoluta* (Cognetti, 1953); *Myrianida dentalia* (Imajima, 1966); *Myrianida edwarsi* (Saint-Joseph, 1887); *Myrianida flava* Nygren, 2004; *Myrianida hesperidium* (Claparède, 1868); *Myrianida inermis* (Saint-Joseph, 1887); *Myrianida irregularis* (Imajima & Hartman, 1964); *Myrianida juventudensis* (San Martín, 1994); *Myrianida langerhansi* (Gidholm, 1967); *Myrianida longoprimicirrata* (López, San Martín & Jiménez, 1997); *Myrianida mediterranea* Çinar & Gambi, 2005; *Myrianida mulidenticulata* (Westheide, 1974); *Myrianida pachycera* (Augener, 1913); *Myrianida pentadentata* (Imajima, 1966); *Myrianida phyllocera* Augener, 1918; *Myrianida pinnigera* (Montagu, 1808); *Myrianida prolifera* (O. F. Müller, 1788); *Myrianida pulchella* Day, 1953; *Myrianida quindecimdentata* (Langerhans, 1884); *Myrianida rainiroaensis* (Hartmann-Schröder, 1992); *Myrianida rubropunctata* (Grube, 1860); *Myrianida spinoculata* (Imajima, 1966).

Bibliography. Potts (1911); Okada (1935, 1937); Gidholm (1965); Hamond (1974); Schiedges (1979a, 1979b); Qian & Chia (1989); Nygren (2004); Nygren & Pleijel (2007).

Genus ***Pachiprocerastea*** Nygren, 2004

Pachyprocerastea Nygren, 2004: 100.

Type-species. *Procerastea hydrozoicola* Hartmann-Schröder, 1992.

Diagnosis. Body of small size, with numerous chaetigers, cylindrical, ventrally flattened. Ciliation unknown. Anterior half of body articulated. Prostomium with 4 eyes. Palps fused. Nuchal epaulettes small, extending over anterior part of peristomium. Three antennae. Two pairs of tentacular cirri. Cirrophores on tentacular cirri and first dorsal cirri present; cirrophores otherwise absent. All appendages cylindrical. Parapodial lobes rounded-conical, small to medium in size. Dorsal bayonet chaetae, thick, distally denticulated. Compound chaetae on ventral position and some simple chaetae on parapodia; simple chaetae with small, difuse denticulation along “fusion line”. Pharynx with sinuation anterior to proventricle. Details of trepan unknown. Reproduction by schizogamy, by anterior scissiparity.

Species and distribution. Only the type-species is known, from New Caledonia, associated on calcified hydrocorals and hydrozoans.

Bibliography. Hartmann-Schröder (1992); Nygren (2004).

Genus ***Paraproceraea*** Nygren, 2004

Paraproceraea Nygren, 2004: 104.

Type-species. *Autolytus (Autolytus) tamanus* Imajima, 1966.

Diagnosis. Body of medium size, with numerous chaetigers, cylindrical, ventrally flattened. Ciliation almost unkown, anterior segments tri-articulated in appearance. Prostomium with 4 eyes. Palps fused. Nuchal epaulettes to half of chaetiger 3. Three antennae. Two pairs of tentacular cirri. All appendages cylindrical. Parapodial lobes rounded, small. Dorsal bayonet chaetae, subdistally denticulated, and compound chaetae with bidentate blades. Pharynx with sinuation anterior and lateral to anterior half of proventricle. Trepan with 90 small subequal teeth. Reproduction unknown.

Species and distribution. Only is known the type-species, from Japan.

Bibliography. Imajima (1966a); Nygren (2004).

Genus ***Paraprocerastea*** San Martín & Alós, 1989

Paraprocerastea San Martín & Alós, 1989: 872.

Type-species. *Paraprocerastea crocantinae* San Martín & Alós, 1989

Diagnosis. Body small, with few chaetigers, cylindrical, ventrally flattened. Ciliation unkown. Prostomium with 4 eyes. Palps fused. Nuchal epaulettes unknown. Three antennae. Two pairs of tentacular cirri. Antennae, tentacular cirri and dorsal cirri of first chaetiger, moderately long, more or less club-shaped; remaining dorsal cirri small, egg-shaped. Parapodial lobes rounded, small. All chaetae simple, with small denticulation present along “fusion line” on some, bidentate with small distal tooth. Bayonet chaetae thick, distally denticulated. Pharynx with single minute sinuation anterior to proventricle. Trepan arranged in 1 ring, with 19-23 equal teeth. Basal ring absent; infradentale spines absent. Two anal cirri. Reproduction unknown.

Species and distribution. Only known the type-species, from Mediterranean coast o Spain.

Bibliography. San Martín & Alós (1989); Nygren (2004).

Genus ***Planicirrata*** Nygren, 2004

Planicirrata Nygren, 2004: 102.

Type-species. *Myrianida proceraeae* Hartmann-Schröder & Rosenfeldt, 1990.

Diagnosis. Body of medium size, with numerous chaetigers, cylindrical, ventrally flattened. Ciliation unkown. Prostomium with 4 eyes. Palps fused, small. Nuchal epaulettes reaching end of tentacular segment. Three antennae (lost on the single specimen known). Two pairs of tentacular cirri. Dorsal cirri lanceolated, flattened. Parapodial lobes rounded conical, small. Dorsal bayonet chaetae thick, distally expanded, distally denticulated. Compound chaetae with bidentate blades, small distal tooth. Pharynx with 3 sinuations. Trepan with about 30 small, equal teeth. Basal ring absent. Reproduction by schizogamy, by anterior scissiparity.

Species and distribution. Only known the type-species, from Antarctica.

Bibliography. Hartmann-Schröder & Rosenfeldt (1990); Nygren (2004).

Genus ***Proceraea*** Ehlers, 1864

Proceraea Ehlers, 1864: 256.

Amytis Savigny, 1822

Polynice Savigny, 1822

Nereisyllis Blainville, 1828

Polybostrichus Örsted, 1843

Stephanosyllis Claparède, 1864

Pteroautolytus Ehlers, 1907

Regulatus Imajima, 1966

Type-species. *Proceraea picta* Ehlers, 1864

Diagnosis. Body of small to large size, with numerous chaetigers, cylindrical, ventrally flattened. Colour pattern often characteristic. Ciliation only present on prostomium, nuchal epaulettes, and ventrally on few segments. Prostomium with 4 eyes, sometimes 2 eyespots. Palps completely fused. Nuchal epaulettes extended from half of persitomium to end of chaetiger 2. Three antennae, median antenna inserted medially on prostomium; lateral antennae on anterior margin. Two pairs of tentacular cirri. Cirrophores present on tentacular cirri and first dorsal cirri, otherwise absent. Anterior appendages cylindrical, dorsal cirri cylindrical or ovoid to egg shaped. Parapodial lobes small to medium in size, rounded to conical. Dorsal bayonet chaetae thick, distally denticulated (thin, subdistally denticulated in one species) and compound chaetae with

bidentate blades. Pharynx with single to multiple sinuations. Trepan arranged in 2 rings, either 1 large tooth alternating with 1 small, or 1 large alternating with 2 small, or 2 large alternating with 1 small, or 1 large alternating with 2-4 small. Number of teeth either 18, 24, 27, or 34-44. Basal ring present; infradental spines absent. Pygidium with 2 anal cirri, without median papilla. Reproduction schyzogamy, by anterior scissiparity.

Species and distribution. The genus is cosmopolitan. Numerous species. *Proceraea anopla* (Monro, 1933); *Proceraea aurantiaca* Claparède, 1868; *Proceraea bifidentata* Ben-Eliahu, 1977; *Proceraea boreata* (Imajima, 1966); *Proceraea cornuta* (Agassiz, 1862); *Proceraea fasciata* (Bosc, 1802); *Proceraea filiformis* Hartmann-Schröder, 1989; *Proceraea gigantea* Nygren & Gidholm, 2001; *Proceraea hanssoni* Nygren, 2004; *Proceraea longilappeta* (Imajima, 1966); *Proceraea madeirensis* Nygren, 2004; *Proceraea micropedata* (Hartmann-Schröder, 1962); *Proceraea misakiensis* (Imajima, 1966); *Proceraea monoceros* (Ehlers, 1907); *Proceraea mukaishima* (Imajima, 1966); *Proceraea nigropunctata* Nygren & Gidholm, 2001; *Proceraea okadai* (Imajima, 1966); *Proceraea paraurantiaca* Nygren, 2004; *Proceraea penetrans* (Wrigth & Woodwick, 1977); *Proceraea picta* Ehlers, 1864; *Proceraea pleijeli* Nygren, 2004; *Proceraea prismatica* (O. F. Müller, 1776); *Proceraea rubroproventriculata* Nygren & Gidholm, 2001; *Proceraea scapularis* (Grube, 1864); *Proceraea setoensis* (Imajima, 1966); *Proceraea vulgaria* (Imajima, 1966).

Bibliography. Agassiz (1862); Okada (1937); Gidholm (1965); Nygren & Gidholm (2001); Nygren (2004).

Genus ***Procerastea*** Langerhans, 1884

Procerastea Langerhans, 1884: 249.

Type-species. *Procerastea nematodes* Langerhans, 1884.

Diagnosis. Body small to medium in size, with numerous chaetigers, cylindrical, ventrally flattened. Ciliation absent, except for nuchal epaulettes. Prostomium with 4 eyes. Palps fused, small, reduced. Nuchal epaulettes maximally extending to end of peristomium. Three antennae; median antenna inserted medially on Prostomium, lateral antennae on anterior margin. Two pairs of tentacular cirri. Dorsal cirri only present on first chaetiger; appendages club shaped or cylindrical. Parapodial lobes rounded, very small. Except for bayonet chaetae, simple chaetae present on chaetigers 1-4, or in all chaetigers. Compound chaetae present from chaetiger 1, chaetiger 2, or absent. Both simple and compounds uni- or bidentate with small distal tooth. Bayonet chaetae thick,

distally dilated, distally denticulated. Pharynx with single small sinuation, or with one to several sinuations, anterior to proventricle. Trepan arranged in 1 ring, with 6-30 equal teeth. Basal ring absent; infradentale spines absent. Two anal cirri. Reproduction by schizogamy by anterior scisiparity.

Species and distribution. Five species, the genus is cosmopolitan. *Procerastea australiensis* Hartmann-Schröder, 1987; *Procerastea halleziana* Malaquin, 1893; *Procerastea nematodes* Langerhans, 1884; *Procerastea parasimpliseta* Hartmann-Schröder, 1992; *procerastea simpliseta* Hartmann-Schröder, 1990.

Bibliography. Potts (1911); Allen (1921); Okada (1937); Giholm (1965; 1967); Hamond (1974); Nygren (2004).

Genus ***Virchowia*** Langerhans, 1879

Virchowia Langerhans, 1879: 582.

Autosyllis Imajima & Hartman, 1964

Type-species. *Virchowia clavata* Langerhans, 1879.

Diagnosis. Body of small size, cylindrical, ventrally flattened, with moderate number of chaetigers. Ciliation present on prostomium and nuchal eppauletes. Prostomium with 4 eyes, and 2 eyes spots on some species. Palps fused at base. Nuchal epaulettes originating from backside of prostomium, entending to between end of chaetiger 1 and end of chaetiger 3. Three antennae; median antenna inserted medially on prostomium, lateral antennae on anterior margin. Two pairs of tentacular cirri. Cirri, cirrophores, and cirrostyles alternate in length, and shape. Appendages cylindrical or club-shaped. Parapodial lobes rounded-conical, small to medium in size. Dorsal bayonet chaetae, thick, distally dilated with distal denticulation. Compound chaetae with small distal tooth, sometimes minute; blade serration absent or present; on one species, blades and shafts fussioned forming simple chaetae. Pharynx with single to multiple sinuations anterior and lateral to proventricle. Trepan arranged in a single ring, with equal or unequal teeth; basal ring present; infradentale spines present. Pygidium with 2 anal cirri, without median papilla. Reproduction by schizogamy, by anterior scissiparity.

Species and distribution. Six species; the genus is cosmopolitan. Several species are associated with hydrozoans. *Virchowia branchiata* (Averincev, 1972); *Virchowia clavata* Langerhans, 1879; *Virchowia japonica* (Imajima & Hartman, 1964); *Virchowia longipharyngea* (Hartmann-Schröder, 1989); *Virchowia pectinans* (Hartmann-Schröder, 1983); *Virchowia spirifer* (Augner, 1913).

Bibliography. Nygren (2004).

Subfamily **Exogoninae** Langerhans, 1879

Diagnosis. Body cylindrical, size from minute to small. Palps fused all along their lengths or at least fused to half. Three antennae, usually short (sometimes extending beyond palps in few species; one species lacking antennae). Four lensed eyes and sometimes two anterior eyespots (few genera with only two eyes). One or two pairs of tentacular cirri, typically short. Nuchal organs consist in two dorsolateral, densely ciliated grooves between prostomium and peristomium. Pharynx straight, with a middorsal, anterior tooth. Dorsal cirri typically short to papilliform, smooth. Reproduction by epigamy and brooding of eggs, some genera dorsally by means of capillary notochaetae, other genera ventrally, attaching eggs and juveniles on nephridial pore.

Apomorphies. The subfamily is defined by one uncontradicted apomorphy: the shape of anal cirri. The group also shows several apomorphies with some reversials: shape of antennae, onion shaped or fusiform dorsal cirri, presence of dorsal simple chaetae from the anterior segments, and the palps totally or practically fused.

Key to genera

Key based on reproductive and morphological characters

1.- Females brooding dorsally.....2

.- Females brooding ventrally, developing juveniles, or viviparous 5

2.- Two pairs of tentacular cirri……3

.- Single pair of tentacular cirri……..4

3.- Body smooth. Antennae and dorsal cirri relatively long.....*Salvatoria*

.- Body papillated. Dorsal cirri shorter…….…….……*Cicese*

4.- Some dorsal cirri with a retractile cirrostyle. Antennae short. Pharynx relatively long and wide; pharyngeal tooth usually located far from anterior margin. Compound chaetae always with short, unidentate blades.....*Prosphaerosyllis*

.- Antennae and dorsal cirri more or less elongate, without distal cirrostyle. Pharynx relatively slender; pharyngeal tooth usually located near anterior margin. Compound chaetae with elongate blades, bidentate, unidentate and bidentate, or unidentate.....

.....…….....*Erinaceusyllis*

5.- Body smooth.....6

.- Body covered with papillae.....*Sphaerosyllis*

6.- Two pairs of tentacular cirri.....……7

.- Single pair of tentacular cirri.....8

7.- Pharynx and proventricle distinctly long. Antennae, tentacular and dorsal cirri filiform, long……...……...…Genus 1

.- Pharynx and proventricle short. Appendages short, bottle-shaped……*Brania*

7.- Palps fused on the basal half to 2/3. Dorsal cirri bowling-pin shaped. Distinct parapodial glands.....*Parapionosyllis*

.- Palps usually fused all along their length or with terminal notch. Dorsal cirri small, papilliform. Parapodial glands indistinct or minute, apparently absent.....……...8

8.- Compound chaetae with tapering, elongated, bidentate falcigers, both teeth similar, and, sometimes, some compound chaetae on each parapodium with elongate, spiniger-like blade. Some species viviparous…….....*Parexogone*

.- Different compound chaetae, with both elongated, spiniger-like blades and other with short falcigers, or blades missing, sometimes fused to shafts. ……*Exogone*

Key based exclusively on morphological features

1.- Two pairs of tentacular cirri.....2

.- Single pair of tentacular cirri.....5

2.- Body papillated……..……..*Cicese*

.- Body without papillae…….……..3

3.- Pharynx and proventricle distinctly long. Antennae, tentacular and dorsal cirri relatively long, filiform .....Genus 1

.- Pharynx and proventricle shorter. Appendages short to very short, papilliform.....4

4.- Palps fused on basal half to 2/3. Dorsal cirri bowling-pin shaped or truncate. Parapodial glands distinct, sometimes inside dorsal cirri. Acicula distally rounded, apparently hollow at tip. Pharynx slender, with distal soft papillae. Pharyngeal tooth conical, located at opening.....*Brania*

.- Palps joined all along their length or mostly by a dorsal membrane. Dorsal cirri spindle-shaped, usually elongate. Parapodial glands absent. Acicula acuminate. Pharynx and proventricle long and wide; usually without papillae on pharyngeal opening. Pharyngeal tooth rhomboidal to ovate, usually located far from pharyngeal opening.....*Salvatoria*

5.- Body without papillae.....6

.- Body papillate.....8

6.- Palps fused on basal half to 2/3. Dorsal cirri bowling-pin shaped. Parapodial glands distinct. Dorsal simple chaetae distally serrated.....*Parapionosyllis*

.- Palps usually fused all along their length or with a distal, short notch. Dorsal cirri small, papilliform. Parapodial glands indistinct. Different dorsal simple chaetae.....7

7.- Compound chaetae with tapering, elongated, bidentate falcigers, both teeth similar, and, sometimes, some compound chaetae on each parapodium with elongate, spiniger-like blade…….....*Parexogone*

.- Different compound chaetae, with both elongated, spiniger-like blades and other with short falcigers, or blades fused to shafts or missing……*Exogone*

8.- Prostomium with 4 eyes, without eyespots. Proventricle short, with few large muscular bands. Pharynx slender; pharyngeal tooth small, conical, located on anterior rim on pharynx. Antennae and dorsal cirri flask- to onion-shaped. Acicula distally with tip forming a right angle.....*Sphaerosyllis*

.- Four eyes and 2 anterior eyespots on prostomium. Proventricle barrel-shaped, long and relatively wide, with numerous, slender muscular bands. Pharynx relatively large. Acicula acuminate.....9

9.- Pharynx distinctly wide, without papillae. Pharyngeal tooth rhomboidal to oval, long, usually located far from anterior rim. Antennae and dorsal cirri similar to *Sphaerosyllis*, but typically having an elongate cirrophore and a retractile cirrostyle. Compound chaetae always with short, unidentate falcigers.....*Prosphaerosyllis*

.- Pharynx proportionally more slender, sometimes with soft papillae surrounding opening. Pharyngeal tooth small, located near anterior rim. Antennae and dorsal cirri elongate, but sometimes similar to those of *Sphaerosyllis*, always without retractile cirrostyle. Compound chaetae usually with elongate blades bidentate, bidentate and unidentate, or unidentate.....*Erinaceusyllis*

Genus 1 Aguado & San Martín, in prep.

Type-species. *Brania gallagheri* Perkins, 1981:1084.

Diagnosis. Body small to medium size, slender, with numerous segments (up around 60). Prostomium with 2 pairs of eyes, 3 filiform, elongated antennae. Palps fused for about their basal 1/3, and the remaining distal 2/3 free. Two pairs of tentacular cirri, elongated, filiform, similar to antennae. Dorsal cirri on all parapodia, those of chaetiger 1 elongated, similar to antennae and tentacular cirri; remaining dorsal cirri shorter, slender, filiform, slightly longer than parapodial lobes. Parapodia conical sometimes truncate. Parapodial glands absent. Pharynx and proventricle long, through several segments (more than 3). Pharynx provided with an anterior tooth, surrounded by a crown of soft papillae. Compound chaetae with short, unidentate, triangular blades. Aciculae with rounded, slightly hollow tips. Dorsal simple chaetae usually subdistally

serrated. Ventral simple chaetae sigmoid. Mature males with natatory chaetae; mature females brooding eggs and juveniles ventrally, with natatory chaetae.

Remarks. Species of this genus were previously described as belonging to *Brania*. However, they differ with this genus in several characters. Antennae, tentacular cirri and first pair of dorsal cirri are distinctly elongated, these appendages and all dorsal cirri are slender, filiform, instead short and bowl-shaped as they are in *Brania*. The chaetae are also different, with short, triangular blades in Genus 1, and furthermore, the mature, gravid females carry eggs and notochaetae; females in *Brania* only carry eggs (or juveniles) but not natatory chaetae, which are exclusive of males.

Species and distribution. Only two species, from Northamerican Atlantic coast. *Brania gallagheri* Perkins, 1981; *Brania wellfleetensis* Pettibone, 1956.

Bibliography. Perkins (1981); Aguado & San Martín (in prep.).

Genus ***Brania*** Quatrefages, 1866

Brania Quatrefages, 1866: 18.

Type-species: *Exogone pusilla* Dujardin, 1839.

Diagnosis. Body small, slender, with few segments. Prostomium with 2 pairs of eyes and, sometimes, 1 pair of eyespots, 3 bowling-pin to spindle-shaped antennae. Palps fused for about their basal 2/3, and the remaining distal 1/3 free. Two pairs of tentacular cirri, bottle-shaped, truncated or bowling-pin shaped. Dorsal cirri on all parapodia, short, bowling-pin shaped or truncated. Parapodia conical, with a distal, rounded small papilla. Parapodial glands present, sometimes inside dorsal cirri. Pharynx provided with an anterior tooth, surrounded by a crown of soft papillae. Compound chaetae with unidentate blades provided with subdistal spines and rounded tips; aciculae with rounded, slightly hollow tips. Dorsal simple chaetae usually subdistally serrated. Ventral simple chaetae sigmoid, usually unidentate. Mature males with natatory chaetae; mature females brooding eggs and juveniles ventrally, without natatory chaetae.

Species and distribution. The genus is known from the temperate and tropical waters. *Brania arminii* (Langerhans, 1881); *Brania articulata* Hartmann-Schröder, 1982; *Brania furcelligera* (Augener, 1913); *Brania glandulosa* Hartmann-Schröder, 1980; *Brania pusilla* (Dujardin, 1851); *Brania rhopalophora* (Ehlers, 1897).

Bibiography. San Martín (2003); San Martín (2005).

Genus ***Cicese*** Díaz-Castañeda & San Martín, 2001

Cicese Díaz-Castañeda & San Martín, 2001: 712-714.

Type-species: *Cicese sphaerosylliformis* Díaz-Castañeda & San Martín, 2001.

Diagnosis. Body small to minute, more or less densely covered by papillae, usually small, short, scarce, sometimes also distributed on cirri and parapodia. Prostomium with 3 antennae, 4 lensed eyes and 2 anterior eyespots. Peristomium usually large, covering posterior margin of prostomium, forming 2 dorso-lateral wings covering nuchal organs; 2 pairs of tentacular cirri. Dorsal cirri on chaetiger 2 present. Antennae, tentacular cirri and dorsal cirri spindle-shaped to pyriform, with bulbous bases and slender tip. A pair of anal cirri similar to dorsal cirri, usually longer. Compound chaetae heterogomph, with blades of different sizes, bidentate; capillary dorsal and ventral simple chaetae present. Middorsal pharyngeal tooth small, located near anterior margin, surrounded by a crown of papillae around opening. Proventricle long and wide, barrel-shaped, with numerous, slender muscle cell rows (15-22). Mature males with natatory chaetae; females brooding eggs dorsally, by means of capillary notochaetae.

Species and distribution. Only the type-species is currently known.

Bibliography: Díaz-Castañeda & San Martín (2001).

Genus ***Erinaceusyllis*** San Martín, 2005.

Erinaceusyllis San Martín, 2005: 73.

Type-species: *Sphaerosyllis erinaceus* Claparède, 1863.

Diagnosis. Body small to minute, more or less densely covered by papillae, usually small, short, scarce, sometimes also distributed on cirri and parapodia. Prostomium with 3 antennae, 4 lensed eyes and 2 anterior eyespots. Peristomium usually large, covering posterior margin of prostomium, sometimes forming 2 dorso-lateral wings covering nuchal organs; single pair of tentacular cirri. Dorsal cirri on chaetiger 2 absent or present, depending upon the species, usually absent. Antennae, tentacular cirri and dorsal cirri spindle-shaped to pyriform, with slightly bulbous bases and short to moderately long tip. A pair of anal cirri similar to dorsal cirri, usually longer. Compound chaetae heterogomph, with blades short or long, sometimes long and slender, bidentate, bidentate and unidentate, or unidentate. Pharyngeal tooth small, conical to romboidal, located near anterior margin, sometimes near middle of pharynx; pharynx usually without papillae around opening, but present on larger species. Proventricle long and wide, barrel-shaped, with numerous, slender muscle cell rows

(15-22). Mature males with natatory chaetae; females brooding eggs dorsally, by means of capillary notochaetae.

Species and distribution. The genus is cosmopolitan. *Erinaceusyllis belizensis* (Russell, 1989); *Erinaceusyllis bidentata* (Hartmann-Schröder, 1974); *Erinaceusyllis bilobata* (Perkins, 1981); (?) *Erinaceusyllis breviforns* (Webster & Benedict, 1884); *Erinaceusyllis centroamericana* (Hartmann-Schröder, 1959); *Erinaceusyllis cirripapillata* San Martín, 2005; *Erinaceusyllis cryptica* (Ben-Eliahu, 1977); *Erinaceusyllis erinaceus* (Claparède, 1863); *Erinaceusyllis ettiennei* San Martín, 2005; *Erinaceusyllis hartmannschroederae* San Martín, 2005; *Erinaceusyllis hermaphrodita* Westheide, 1990; *Erinaceusyllis horrockensis* (Hartmann-Schröder, 1981); *Erinaceusyllis kathrynae* San Martín, 2005; *Erinaceusyllis longilamina* Russell, 1989; *Erinaceusyllis mussismiliaicola* (Nogueira, San Martín & Amaral, 2001); *Erinaceusyllis nuchalata* Hartmann-Schröder, 1960); *Erinaceusyllis opisthodentata* (Hartmann-Schröder, 1987); *Erinaceusyllis parvoculata* Russell, 1989; (?) *Erinaceusyllis perspicax* (Ehlers, 1908); *Erinaceusyllis renaudae* (Hartmann-Schröder, 1958); *Erinaceusyllis ridgensis* Blake & Hilbig, 1990; *Erinaceusyllis ruthae* San Martín, 2004; *Erinaceusyllis serrata* Hartmann-Schröder, 1974; *Erinaceusyllis serratosetosa* (Hartmann-Schröder, 1982); *Erinaceusyllis subterranea* (Hartmann-Schröder, 1960); *Erinaceusyllis subterranea* (Hartmann-Schröder, 1965) (Homonimy).

Bibliography. Russell (1989); San Martín (2003, 2005).

Genus ***Exogone*** Örsted, 1845

Exogone Örsted, 1845b: 20.

Cystonereis Kölliker in Koch, 1846

Exagone Milne Edwards, 1851

Exogona Dujardin, 1851

Exonita Hartman & Fauchlad, 1971

Exotokas Ehlers, 1864

Gossia Quatrefages, 1865

Microsyllis Claparède, 1863

Oophylax Ehlers, 1864

Spermosyllis Claparède, 1864

Sylline Claparède, 1864

Syllia Quatrefages, 1865

Gossia Quatrefages, 1866

Schmardia Quatrefages, 1866

Paedophylax Claparède, 1868

Paedophyllax Fage, 1906

Type-species: *Exogone naidina* Örsted, 1845.

Diagnosis. Body small, slender, more or less filiform. Prostomium with 3 antennae, exceptionally without antennae; usually 4 eyes, sometimes also with 2 eyespots, occasionally without eyes. Palps well developed, completely fused to each other or with terminal notch. Single pair of minute tentacular cirri. Dorsal cirri usually small, papilliform to oval, present on all segments or absent on chaetiger 2 in adults of some species. Usually compound chaetae and dorsal and ventral simple chaetae; sometimes blades fused to shafts or without blades, forming simple chaetae. Two usually long anal cirri present. Body surface smooth. Pharynx with anterior margin surrounded by soft lobes, with anterior tooth. Mature females carrying eggs ventrally, developing to embryos and juveniles, lacking capillary notochaetae (natatory chaetae); mature males with long natatory chaetae; some species are viviparous.

Species and distribution. The genus is cosmopolitan. *Exogone acerata* San Martín & Parapar, 1990; *Exogone aquadulcensis* Pascual, Núñez & san Martín, 1996; *Exogone africana* Hartmann-Schröder, 1974; *Exogone anomalochaeta* Benham, 1921; *Exogone arenosa* Perkins, 1981; *Exogone anomalochaeta* Benham, 1921; *Exogone aristata* Hartmann-Schröder, 1982; *Exogone arrakatarkoola* San Martín, 2005; *Exogone bondi* Ruíz-Ramírez & Salazar-Vallejo, 2001; *Exogone breviantennata* Hartmann-Schröder, 1959; *Exogone brevifalcigera* Hartmann-Schröder, 1990; *Exogone brevipes* Claparède, 1864; *Exogone dieteri* San Martín, 2004; *Exogone dispar* (Webster, 1879); *Exogone fungopapillata* Zhao & Wu, 1991; *Exogone fustifera* Haswell, 1920; *Exogone goorapuranga* San Martín, 2005; *Exogone haswelli* San Martín, 2005; *Exogone heterosetoides* Hartmann-Schröder, 1979; *Exogone heterosetosa* McIntosh, 1885; *Exogone ingridae* San Martín, 2005; *Exogone jangopapillata* Zhao & Wu, 1991; *Exogone kooreborongi* San Martín, 2005; *Exogone longiantennata* Hartmann-Schröder, 1979; *Exogone longicornis* Westheide, 1974; *Exogone longispinulata* San Martín, 1991; *Exogone lopezi* San Martín, Ceberio & Aguirrezabalaga, 1996; *Exogone lourei* Berkelei & Berkeley, 1938; *Exogone marisae* Pascual, Núñez & San Martín, 1996; *Exogone mompasensis* Martínez, Adarraga & San Martín, 2002; *Exogone multisetosa* Friedrich, 1956; *Exogone naidina* Örsted, 1845; *Exogone naidinoides* Westheide, 1974; *Exogone*

oculata (Hartmann & Fauchald, 1971); *Exogone peseudolourei* San Martín 1991; *Exogone rolani* San Martín 1991; *Exogone rostrata* Naville, 1933; *Exogone simplex* Hartmann-Schröder, 1960; *Exogone sorbei* San Martín, Ceberio & Aguirrezabalaga, 1996; *Exogone tatarica* Annenkova, 1938; *Exogone uniformis* Hartman, 1961; *Exogone verugera* (Claparède, 1868).

Bibliography. San Martín (1991, 2003, 2005); Böggeman & Westheide (2004).

Genus ***Parapionosyllis*** Fauvel, 1923

Parapionosyllis Fauvel, 1923: 289.

Type-species: *Pionosyllis gestans* Pierantoni, 1903.

Diagnosis. Body small to minute. Prostomium with 2 pairs of eyes and, sometimes, a pair of eyespots, 3 bowling-pin shaped antennae. Palps partially fused, distal half or 1/3 free of each other. Single pair of tentacular cirri, bottle- or bowling-pin shaped, located latero-ventrally. Dorsal cirri on all parapodia, short, bowling-pin shaped. Parapodial lobes conical, with a small, thin distal rounded papilla. Parapodial glands present. Dorsal simple chaetae usually subdistally serrated. Ventral simple chaetae sigmoid, usually unidentate. Pharynx provided with an anterior tooth, surrounded by soft papillae. Compound chaetae with unidentate blades provided with a subdistal spine and rounded tip; aciculae with a rounded, slightly hollowed tip. Mature males with natatory chaetae, mature females brooding eggs or juveniles ventrally, lacking natatory chaetae.

Remarks. *Parapionosyllis* is identical to *Brania*, but having a single pair rather than two pairs of tentacular cirri.

Species and distribution. The genus is known from the temperate and tropical waters. *Parapionosyllis abriguensis* Riera, Núñez & Brito, 2006; *Parapionosyllis brevicirra* Day, 1954; *Parapionosyllis cabezali* Parapar, San Martín & Moreira, 2000; *Parapionosyllis elegans* (Pierantoni, 1903); *Parapionosyllis floridana* San Martín, 1991; *Parapionosyllis gestans* (Pierantoni, 1903); *Parapionosyllis labronica* Cognetti, 1965; *Parapionosyllis longicirrata* (Webster & Benedict, 1884); *Parapionosyllis macaronesiensis* Brito, Núñez & San Martín, 2000; *Parapionosyllis manca* Treadwell, 1931; *Parapionosyllis minuta* (Pierantoni, 1903); *Parapionosyllis papillosa* (Pierantoni, 1903); *Parapionosyllis parapionosylliformis* (Hartmann-Schröder, 1962); *Parapionosyllis richardi* San Martín, 2005; *Parapionosyllis retrodens* (Ehlers, 1897); *Parapionosyllis uebelackerae* San Martín, 1991; *Parapionosyllis winnunga* San Martín, 2005.

Bibliography. Pierantoni (1903); Fauvel (1923); Cognetti (1965); Lewbart & Riser (1996); San Martín (2003, 2005)

Genus ***Parexogone*** Mesnil & Caullery, 1918

Parexogone Mesnil & Caullery, 1918: 125.

Exogonella Hartman, 1961: 74.

? *Spermosyllis* Claparède, 1864

Type species: *Paedophylax hebes* Webster & Benedict, 1884.

Diagnosis. Body small, meiofaunal, surface smooth. Prostomium with 3 antennae; usually 4 eyes, sometimes also with 2 eyespots. Palps well developed, completely fused to each other or with terminal notch. Single pair of minute tentacular cirri. Dorsal cirri usually small, papilliform to oval, present on all segments or absent on chaetiger 2 in adults of some species. Compound chaetae with heterogomph articulations, falcigers all similar in shape and blade length, sometimes psudospinigers (elongate falcigers) with shaft tips simple, blades relatively similar to falcigers but longer. Dorsal simple chaetae similar throughout body, tips unidentate or bidentate, with both teeth similar. Ventral simple chaetae on posterior parapodia. Pharynx with anterior margin surrounded by soft lobes, with anterior tooth. Two usually long anal cirri present. Mature females carrying eggs ventrally, developing to embryos and juveniles, lacking capillary notochaetae (natatory chaetae); mature males with long natatory chaetae; some species viviparous.

Species and distribution. The genus is cosmopolitan. *Parexogone annamurrayae* San Martín, 2005; *Parexogone anseforbasensis* Böggemann & Westheide, 2004; *Parexogone atlantica* (Perkins, 1981); *Parexogone campoyi* (San Martín, Ceberio & Aguirrezabalaga, 1996); *Parexogone caribensis* (San Martín, 1991); *Parexogone cognettii* (Castelli, Badallamenti & Lardicci, 1987); *Parexogone convoluta* (Campoy, 1982); *Parexogone exmouthensis* (Hartmann-Schröder, 1980); *Parexogone fauveli* (Cognetti, 1961); *Parexogone furcifera* (Eliason, 1962); *Parexogone gambiae* (Lanera, Sordino & San Martín, 1994); *Parexogone hebes* (Webster & Benedict, 1884); *Parexogone heboides* Ben-Eliahu, 1977; *Parexogone homosetosa* Hartmann-Schröder, 1965; *Parexogone longicirris* (Webster & Benedict, 1887); *Parexogone meridionalis* (Cognetti, 1955); *Parexogone microtentaculata* Westheide, 1974; *Parexogone minuscula* (Hartman, 1953); *Parexogone molesta* Banse, 1972; *Parexogone normalis* Day, 1963; *Parexogone obtusa* (Hartmann-Schröder & Rossenfelt, 1988); *Parexogone parahebes* Hartmann-Schröder, 1965; *Parexogone parahomoseta* (Hartmann-Schröder,

1974); *Parexogone patriciae* San Martín, 2005; *Parexogone penelopeae* San Martín, 2005; *Parexogone remanei* Storch, 1966; *Parexogone sanmartini* Ruíz-Ramírez & Salazar-Vallejo, 2001; *Paraexogone seichellensis* Böggemann & Westheide, 2004; *Parexogone sexoculata* Hartmann-Schröder, 1979; *Parexogone tasmanica* Hartmann-Schröder, 1989; *Parexogone wilsoni* San Martín, 2005; *Parexogone wolfi* San Martín, 1991.

Bibliography. Pocklington & Hutchenson (1983); San Martín (1991, 2003, 2005); Böggemann &Westheide (2004).

Genus ***Prosphaerosyllis*** San Martín, 1984

Sphaerosyllis (Prosphaerosyllis) San Martín, 1984: 377.

Type-species: *Sphaerosyllis xarifae* Hartmann-Schröder, 1960.

Diagnosis. Body small, with few segments, provided with dorsal and ventral papillae, also present on cirri and parapodia; usually covered by detritus; sometimes, some dorsal or ventral papillae long (macropapillae). Prostomium with 3 small, short antennae, 4 eyes, and 2 anterior eyespots, usually partially covered dorsally by peristomium, some species with the prostomium completely retracted inside peristomium. Palps fused along their length, short, slightly ventrally folded, provided with small papillae. Single pair of tentacular cirri, located ventro-laterally. Two small nuchal organs with ciliated lateral clefts, usually covered by peristomium and difficult to see. Antennae, tentacular and dorsal cirri short, pyriform to bulbous, with sphaerical bases and short tips that are usually retractile inside bases, especially in midbody and posterior parapodia; tips sometimes papilliform and short; dorsal cirri present on all parapodia. Parapodial glands absent. Parapodia with compound, heterogomph chaetae with unidentate, short, falcate blades; dorsal and ventral simple, capillary, unidentate chaetae on some parapodia. Acicula usually solitary, acuminate, sometimes slightly modified. Pharynx long and wide, usually without papillae around opening; pharyngeal tooth romboidal to oval, located posteriorly from anterior margin of pharynx, sometimes on middle of pharynx. Proventricle long and wide, similar in size to pharynx, provided with numerous, slender muscle cell rows. Reproduction by epigamy with dorsal brooding by means of capillary notochaetae; mature males provided with long, thin natatory chaetae on mature segments.

Species and distribution. The genus is cosmopolitan. *Prosphaerosyllis adelae* (San Martín, 1984); *Prosphaerosyllis annulata* Nogueira, San Martín & Fukuda, 2004;

Prosphaerosyllis battiri San Martín, 2005; *Prosphaerosyllis bengalensis* Rao & Ganapati, 1966; *Prosphaerosyllis brandhorsti* Hartmann-Schröder, 1965; *Prosphaerosyllis brevidentata* (Perkins, 1981); *Prosphaerosyllis campoyi* San Martín, Acero, Contonente & Gómez, 1982; *Prosphaerosyllis chinensis* Zhao & Wu, 1991; *Prosphaerosyllis giandoi* Somaschni & San Martín, 1994; *Prosphaerosyllis isabellae* (Nogueira, San Martín & Amaral, 2001); *Prosphaerosyllis joinvillensis* (Hartmann-Schröder & Rosenfeldt, 1988); *Prosphaerosyllis kerguelensis* (McIntosh, 1885); *Prosphaerosyllis longicauda* (Webster & Benedict, 1887); *Prosphaerosyllis longipapillata* (Hartmann-Schröder, 1979); *Prosphaerosyllis magnoculata* (Hartmann-Schröder, 1986); *Prosphaerosyllis brevicirra* (Hartmann-Schröder, 1960); *Prosphaerosyllis multipapillata* (Hartmann-Schröder, 1979); *Prosphaerosyllis nathani* (San Martín & López, 1998); *Prosphaerosyllis palpopapillata* (Hartmann-Schröder & Rosenfeldt, 1992); *Prosphaerosyllis papillosissima* (Hartmann-Schröder, 1979); *Prosphaerosyllis riseri* (Perkins, 1981); *PrsophaeroSyllis semiverrucosa* (Ehlers, 1913); *Prosphaerosyllis sexpapillata* (Hartmann-Schröder, 1979); *Prosphaerosyllis opisthoculata* (Hartmann-Schröder, 1979); *Prosphaerosyllis tetralix* (Eliason, 1920); *Prosphaerosyllis xarifae* (Hartmann-Schröder, 1960).

Bibliography. San Martín (1984, 2003, 2005); Riser (1991).

Genus ***Salvatoria*** McIntosh, 1885

Salvatoria McIntosh, 1885: 188

Grubea Quatrefages, 1866

GrubeoSyllis Verrill, 1900

Protogrubea Czerniavsky, 1881

Pseudobrania San Martín, 1984

Brania.- in part Fauvel 1923; in part Kudenov & Harris, 1995. Not Quatrefages 1866

Type-species. *Salvatoria kerguelensis* McIntosh, 1885.

Diagnosis. Body small with few segments, around 30, surface smooth, usually without colour markings, but some species with red transverse bands on some segments. Prostomium with 3 antennae, 4 eyes and, usually, 2 eyespots. Palps well developed, joined along their length by dorsal membrane, more or less distinct, sometimes with distal, usually short notch. Two pairs of tentacular cirri. Antennae, tentacular cirri and dorsal cirri usually spindle-shaped, proportionally long and slender in comparison with those present in other genera of the subfamily, usually slightly bulbous at their base and

ending with an elongate, acute tip; dorsal cirri present on all segments or absent on chaetiger 2. Parapodia conical, typically ending in 3 rounded, small papillae. Ventral cirri digitiform, shorter than parapodial lobes. Parapodial glands absent. Compound chaetae heterogomph, with blades bidentate, sometimes subdistal tooth small, appearing as unidentate; some parapodia with dorsal and ventral simple capillary chaetae. Acicula usually solitary, acuminate, with long and filiform tip; in some species without tip, appearing distally rounded. Pharynx wide, usually without papillae around the opening, although some larger species have crown of small papillae; usually band of cilia at opening of pharynx; pharyngeal tooth typically romboidal to ovate, located anywhere from near anterior margin to about the middle of pharynx. Proventricle proportionally long and wide, massive, sometimes longer than pharynx but usually of the same length, with numerous, slender muscular rows. Pygidium with two anal cirri, similar to dorsal cirri. Reproduction by epigamy, females brooding eggs by means of capillary notochaetae; mature males provided with long natatory notochaetae.

Species and distribution. The genus is cosmopolitan. *Salvatoria alvaradoi* (San Martín, 1984); *Salvatoria balani* (Hartmann-Schröder, 1960); *Salvatoria breviarticulata* (Nogueira, San Martín & Amaral, 2001); *Salvatoria brevipharyngea* Banse, 1972; *Salvatoria celiae* (Parapar & San Martín, 1992); *Salvatoria clavata* (Claparède, 1863); *Salvatoria concinna* Westheide, 1974; *Salvatoria dolichopoda* (Marenzeller, 1874); *Salvatoria euritmica* (Sardá, 1984); *Salvatoria gracilis* (Hartmann-Schröder, 1960); *Salvatoria heterocirra* (Rioja, 1941); *Salvatoria jonssonii* (Saemundsson, 1918); *Salvatoria kerguelensis* Mc Instosh, 1885; *Salvatoria koorineclavata* San Martín, 2005; *Salvatoria limbata* (Claparède, 1868); *Salvatoria longisetosa* (Hartmann-Schröder, 1979); *Salvatoria longiarticulata* (Nogueira, San Martín & Amaral, 2001); *Salvatoria longisetis* (Fauvel, 1919); *Salvatoria mediodentata* (Westheide, 1974); *Salvatoria neapolitana* (Goodrich, 1930); *Salvatoria nitidula* Verrill, 1900; *Salvatoria nutrix* (Monro, 1936); *Salvatoria opisthodentata* (Hartmann-Schröder, 1979); *Salvatoria pilkena* San Martín, 2005; *Salvatoria quadrioculata* (Augener, 1913); *Salvatoria rugulosa* Verrill, 1900; *Salvatoria russeli* (Ruíz-Ramírez & Salazar-Vallejo, 2001); *Salvatoria swedmarki* (Gidholm, 1962); *Salvatoria uebelackerae* (Ruíz-Ramírez & Salazar-Vallejo, 2001); *Salvatoria vieitezi* (San Martín, 1984); *Salvatoria westheidei* (Ruíz-Ramírez & Salazar-Vallejo, 2001); *Salvatoria yraidae* (San Martín, 1984).

Bibliography. Kuper & Westheide (1998); San Martín (1991, 2003).

Genus ***Sphaerosyllis*** Claparède, 1863

Sphaerosyllis Claparède, 1863: 45.

Type-species: *Sphaerosyllis hystrix* Claparède, 1863.

Diagnosis. Body small, provided with similar dorsal and ventral papillae, sometimes extending to cirri and parapodia, usually covered by detritus. Prostomium with 3 antennae, 4 eyes, without eyespots, usually partially covered dorsally by peristomium. Palps fused all along their length. Single pair of tentacular cirri, located latero-ventrally, directed to anteriorly. Antennae, tentacular and dorsal cirri short, pyriform to bulbous- or flask-shaped, with sphaerical bases and short, slender tips; dorsal cirri absent on chaetiger 2. Parapodial glands usually present and distinct, with fibrillar, hyaline, or granular material. Parapodia with compound, heterogomph chaetae with unidentate, short blades; dorsal and ventral simple, unidentate chaetae on some parapodia. Aciculae usually solitary, thick, distally bent at right angle; sometimes with another straight, slender acicula in anterior parapodia. Pharynx slender, provided with small, soft papillae around opening; pharyngeal tooth conical, on anterior margin. Proventricle short, provided with few (12-20/23), large muscle cell rows. Reproduction by epigamy with incubation; mature males provided with long, thin natatory chaetae; females without natatory chaetae, brooding eggs and juveniles ventrally.

Species and distribution. The genus is cosmopolitan. *Sphaerosyllis aciculata* Perkins, 1981; *Sphaerosyllis antartica* Gravier, 1906; *Sphaerosyllis asiatica* Buzhinskaja, 1980; *Sphaerosyllis austriaca* Banse, 1959; *Sphaerosyllis bardukaciculata* San Martín, 2005; *Sphaerosyllis bifurcata* (Hartmann-Schröder, 1979); *Sphaerosyllis bifurcatoides* (Hartmann-Schröder, 1979); *Spaherosyllis boeroi* Musco, Çinar & Giangrande, 2005; *Sphaerosyllis brasiliensis* Nogueira, San Martín & Amaral, 2001; *Sphaerosyllis bulbosa* Southern, 1914; *Sphaerosyllis capensis* Day, 1953; *Sphaerosyllis claparedei* Ehlers, 1864; *Sphaerosyllis densopapillata* Hartmann-Schröder, 1979; *Sphaerosyllis fortuita* Webster, 1879; *Sphaerosyllis georgeharrisoni* San Martín, 2005; *Sphaerosyllis glandulata* Perkins, 1981; *Sphaerosyllis goorabantennata* San Martín, 2005; *Sphaerosyllis gravinae* Somaschini & San Martín, 1994; *Sphaerosyllis hirsuta* Ehlers, 1897; *Sphaerosyllis hystrix* Claparède, 1863; *Sphaerosyllis lateropapillata* Hartmann-Schröder, 1986; *Sphaerosyllis magnidentata* Perkins, 1981; *Sphaerosyllis minima* Hatmann-Schröder, 1960; *Sphaerosyllis papillifera* Naville, 1933; *Sphaerosyllis parabulbosa* San Martín & López, 2002; *Sphaerosyllis pirifera* Claparède, 1868; *Sphaerosyllis piriferopsis* Perkins, 1981; *Sphaerosyllis pygipapillata* Hartmann-

Schröder, 1981; *Sphaerosyllis rotundipapillata* Hartmann-Schröder, 1982; *Sphaerosyllis sanmartini* Böggemann & Westheide, 2004; *Sphaerosyllis sublaevis* Ehlers, 1913; *Sphaerosyllis taylori* Perkins, 1981; *Sphaerosyllis thomasi* San Martín, 1984; *Sphaerosyllis voluntariorum* San Martín, 2005.

Bibliography. Pierantoni (1903); Perkins (1981); San Martín (1984, 2003, 2005).

Subfamily ***Syllinae*** Grube, 1850

Eurysyllinae Hartman, 1964.

Diagnosis. Body cylindrical or dorso-ventrally flattened, size from small to large or very large. Palps basally fused or free at bases (one genus with palps fused almost all their length). Three antennae, usually long, extending beyond palps. Four lensed eyes and sometimes two anterior eyespots (one genus with only one pair eyes.). Two pairs of tentacular cirri, typically long and slender (one genus with single pair). Nuchal organs consists in two dorsolateral, densely ciliated grooves between prostomium and peristomium (one genus with nuchal epaulettes). Pharynx straight, typically with a middorsal, anterior tooth (some exceptions). Dorsal cirri typically long, articulated (few genera with short dorsal cirri formed by a single article). Reproduction by schizogamy.

Apomorphies. The subfamily is defined by two apomorphies: anterior scissyparity and stolons without distinct regions, not showing dimorphism. Schyzogamy in Syllinae is considered as a different process to schyzogamy in Autolytinae.

Remarks. Unfortunately, the reproductive mode is unknown for several terminals (*Paraopisthosyllis* and *Karroonsyllis*). They are transitorily included in the subfamily until we find more information about them.

Key to genera

1.- Only simple chaetae, usually thick……2

.- Compound chaetae and capillary dorsal and ventral chaetae (sometimes some chaetae in midbody appear simple by blade and shafts fussion, but also compound chaetae are present anteriorly)……..……7

2.- Antennae, tentacular and dorsal cirri smooth (very weakly articulated in few species)……...3

.- Appendages articulated…….....4

3.- Two eyes. Chaetae thick and tridentate. Pharyngeal tooth present or absent……..*Haplosyllides*

.- Four eyes. Chaetae relatively slender, ending in a thin tip. Pharyngeal tooth present. Some species and juveniles can have few small compound chaetae……*Alcyonosyllis*

4.- Pharynx slender, coiled, with a trepan. Dorsal cirri short, obscurely articulated…….
……*Parahaplosyllis*

.- Pharynx straight. Dorsal cirri long, articulated (some species can have smooth or weakely articulated dorsal cirri on posterior half of body)……..…..……5

5.- Without trepan…….……*Haplosyllis*

.- Trepan present……..6

6.- Body cylindrical…….…….*Trypanoseta*

.- Body dorso-ventrally flattened……..……*Trypanosyllis* (*Trypanobia*)

7.- Single pair of tentacular cirri. Palps fused almost all their length…….....*Karroonsyllis*

.- Two pairs of tentacular cirri. Palps free or basally fused…….....8

8.- Two nuchal epaulettes, with transversal ridges……*Nuchalosyllis*

.- Without nuchal epaulettes……..……...9

9.- Some or all compound chaetae claw-shaped, with the blades turned 180°. Some species with gills on dorsal surface of some parapodia. Body cylindrical, dorsoventrally flattened or laterally compressed……..……...*Branchiosyllis*

.- Without that kind of compound chaetae. Without gills……..10

10.- Pharyngeal tooth absent…….……..…….11

.- Pharyngeal tooth present……12

11.- Body cylindrical, smooth……..*Inermosyllis*

.- Body dorso-ventrally flattened, with papillae and longitudinal grooves……*Xenosyllis*

12.- Palps free, dorsally divided by a longitudinal groove, appearing as bipartite……..……*Tetrapalpia*

.- Palps free or fused basally, not divided by longitudinal grooves…….……..13

13.- Body small, dorso-ventrally flattened. Antennae, tentacular and dorsal cirri reduced to a single, sphaerical article…….……..14

.- Body of medium to large size, cylindrical or flattened. Appendages with several articles (moniliform) or with single article club-shaped…..……..15

14.- Palps fused. Two rows of dorsal, spherical tubercles, similar to dorsal cirri……...*Eurysyllis*

.- Palps free. Without dorsal tubercles……..……*Plakosyllis*

15.- Dorsal cirri of midbody reduced to a single article, lemmon-shaped, alternating with long, moniliform cirri……..…….....*Parasphaerosyllis*

.- All dorsal cirri moniliform……..…….....16

16.- Trepan present, with or without middorsal tooth……..17

.- Trepan absent…….……18

17.- Body dorsoventrally flattened……*Trypanosyllis*

.- Body cylindrical…….……*Dentatisyllis*

18.- Pharyngeal tooth located posteriorly……..……...19

.- Tooth localed on anterior margin of pharynx……20

19.- Body papillated. Dorsal cirri composed by a single, club-shaped article…….....*Paraopisthosyllis*

.- Body smooth. Dorsal cirri moniliform…….....……...*Opisthosyllis*

20.- Pharyngeal tooth long, slender. Body densely papillated. Thick simple chaetae on posterior parapodia…….....*Rhopalosyllis*

.- Pharyngeal tooth conical, short. Body without papillae over dorsum. Usually compound chaetae (some thick simple chaetae may be present on midbody in some species)……21

21.- Antennae, tentacular and dorsal cirri apparently unarticulated in large specimens (weakly articulated on juveniles). Segments bi- or tri- articulated. Huge species (for the ranging of Syllidae). Dorsal cirri alternating in their position, the longer more dorsally located ….……*Megasyllis*

.- Antennae, tentacular and dorsal cirri more or less articulated. Segments without secondary annuli. Smaller species. Dorsal cirri originating all at the same level……..22

22.- Antennae, tentacular and anterior dorsal cirri articulated, gradually smooth posteriorly (juveniles with antennae and cirri smooth)……..……...Genus 2

.- Antennae, tentacular and dorsal cirri articulated, even in juveniles……...*Syllis*

Genus 2 San Martín, Licher & Aguado, in prep.

Type-species. *Pionosyllis marquesensis* Monro, 1939.

Diagnosis. Body long, robust, dorsally convex, of macrofaunal size. Prostomium with four eyes; usually two lateral swellings; lateral antennae arising from lateral swellings; median antenna inserted on middle of prostomium or anteriorly. Palps large, broad, fused at their bases. Two pairs of tentacular cirri. Antennae, tentacular and anterior dorsal cirri articulated to weakly wrinkled; remaining dorsal cirri irregularly articulated to smooth, slender, long to moderate in length. Parapodia with prechaetal and postchaetal lobes. Compound chaetae heterogomph, with strongly bidentate falcigers, typically both teeth similar, acute. Solitary dorsal and ventral simple capillary chaetae on posterior parapodia; dorsal simple chaetae very thin, much slender than shafts of compound chaetae. Pharynx shorter than proventricle, provided with a crown of soft

papillae and one single tooth, placed anteriorly, slightly back from pharyngeal rim. Reproduction by schizogamic scissiparity by means of sexual stolons, both male and female, with four eyes, four short papilliform antennae, and dorsal cirri smooth.

Remarks. Different species assigned to genera *Pionosyllis* and *Syllis* share similar morphological features. The description of this genus together re-description of several species is currently in preparation.

Species and distribution. *Typosyllis subantennata* (Hartmann-Schröder, 1984); *Pionosyllis marquesensis* (Monro, 1939); *Syllis nipponica* (Imajima, 1966); *Pionosyllis procera* (Hartman, 1965); *Typosyllis glandulosa* (Augener, 1913); *Typosyllis pseudoheterosetosa* Böggemann & Westheide, 2004.

Bibliography. San Martín & Estapé (1993)San Martín *et al.* (submitted b); San Martín *et al.* (in prep.)

Genus ***Alcyonosyllis*** Glasby & Watson, 2001

Alcyonosyllis Glasby & Watson, 2001: 44-45.

Type-species. *Alcyonosyllis phili* Glasby & Watson, 2001.

Diagnosis. Body of medium to large size, with numerous segments. Prostomium with 3 antennae, 2 pair of eyes, and 2 palps. Palps basally fused. Two pairs of tentacular cirri. Antennae, tentacular, anal, and dorsal cirri smooth; some species with very indistinctly articulated cirri on some parapodia. Parapodia conical. Ventral cirri digitiform. Few (2-3) slender, simple, hoocked chaetae with subdistal boss per parapodium; capillary dorsal and ventral simple chaetae absent; some species with small compound chaeta and capillary ventral simple chaeta on some parapodia. Pharynx with middorsal tooth, located on anterior rim; anterior margin of pharynx surrounded by crown of soft papillae. Reproduction by means of stolons.

Species and distribution. The genus is only known from the tropical Pacific. Associated with octocorals. *Alcyonosyllis galsbyi* San Martín & Nishi, 2003; *Alcynosyllis phili* Glasby & Watson, 2001; *Alcyonosyllis onkylochaeta* (Hartmann-Schröder, 1991); *Alcyonosyllis xeniaecola* (Hartman-Schröder, 1993); *Alcyonosyllis exiliformis* (Imajima, 2003).

Bibliography. Glasby & Watson (2001); San Martín & Nishi (2003); Aguado *et al.* (submitted).

Genus ***Branchiosyllis*** Ehlers, 1887

Branchiosyllis Ehlers, 1887: 148.

Type-species: *Branchiosyllis oculata* Ehlers, 1887, by monotypy.

Diagnosis. Body of medium to large size, some species cylindrical, others dorso-ventrally flattened, or laterally compressed, with numerous segments. Prostomium with 4 eyes, and sometimes 2 eyespots, 3 antennae and 2 palps. Palps fused at bases. Two pairs of tentacular cirri. Antennae, tentacular, anal and dorsal cirri distinctly articulated. Parapodia with branchiae or digitiform lobes on some species, absent on most species. Compound chaetae falcigers; blades of some or all chaetae rotated 180°, claw-shaped. Capillary simple chaetae absent. Pharynx with an anterior tooth, surrounded by crown of about 10 soft papillae. Two anal cirri.

Species and distribution. The genus is circuntropical, with one species in the Mediterranean Sea. *Branchiosyllis baringabooreen* San Martín, Hutchings & Aguado, in press; *Branchiosyllis cirropunctata* (Michel, 1909); *Branchiosyllis diazi* Rioja, 1958; *Branchiosyllis exilis* (Gravier, 1900); *Branchiosyllis lamellifera* Verrill, 1900; *Branchiosyllis lorenae* San Martín & Bone, 1999; *Branchiosyllis maculata* (Imajima, 1966); *Branchiosyllis oculata* Ehlers, 1887; *Branchiosyllis orbiniiformis* San Martín, Hutchings & Aguado, in press; *Branchiosyllis pacifica* Rioja, 1941; *Branchiosyllis roldanae* San Martín, Hutchings & Aguado, in press; *Branchiosyllis thylacini* San Martín, Hutchings & Aguado, in press; *Branchiosyllis verruculosa* (Augener, 1913).

Bibliography. Pawlik (1983); Aguado *et al.* (in press); San Martín *et al.* (in press).

Genus ***Dentatisyllis*** Perkins, 1981

Dentatisyllis Perkins, 1981: 1166.

Type-species. *Syllis carolinae* Day, 1973.

Diagnosis. Body of medium to large size (5->10 mm in length), long, with numerous segments. Prostomium with 3 antennae, 2 pairs of eyes and sometimes 1 pair of eyespots, and 2 palps. Palps basally fused. Two pairs of tentacular cirri. Antennae, tentacular, anal, and dorsal cirri distinctly articulated. Parapodial lobes conical. Ventral cirri ovate. Compound chaetae with falcigerous blades, spiniger-like blades present on some species; capillary dorsal and ventral simple chaetae present. Pharynx with middorsal tooth, located on anterior rim; anterior margin of pharynx surrounded by crown of soft papillae and a trepan. Reproduction by means of stolons.

Species and distribution. The genus is circuntropical. *Dentatisyllis carolinae* (Day, 1973); *Dentatisyllis hongkongensis* Ding, Licher & Westheide, 1998; *Dentatisyllis junoyi* López & San Martín, 1992; *Dentatisyllis kiaorensis* (Hartmann-Schröder, 1992); *Dentatisyllis mangalis* Russell, 1995; *Dentatisyllis morrocoyensis* San Martín & Bone, 1999; *Dentatisyllis uebelackerae* Ding, Licher & Westheide, 1998.

Bibliography. Perkins (1981); Ding, Licher & Westheide (1998).

Genus ***Eurysyllis*** Ehlers, 1864

Eurysyllis Ehlers, 1864: 264.

Polymastus Claparède, 1864

Type-species: *Eurysyllis tuberculata* Ehlers, 1864.

Diagnosis. Body small, oval, elongated, strongly dorso-ventrally flattened. Prostomium with 2 pairs of eyes, 3 antennae and 2 spherical palps. Antennae inserted on anterior margin of prostomium; palps inserted ventrally, fused to each other. Dorsum provided with 4 longitudinal rows of spherical tubercles, similar in size and shape to antennae and dorsal cirri, 4 tubercles present on each segment except peristomium, which has 2. Two pairs of tentacular cirri. Antennae, tentacular and dorsal cirri reduced to single spherical article. Ventral cirri short, oval, with minute pores. Two anal cirri similar to dorsal cirri. Compound chaetae with short falcigers; some simple capillary chaetae on posterior parapodia. Pharynx with anterior tooth, surrounded by crown of about 10 soft papillae and trepan of minute, indistinct teeth. Proventricle short. Schizogamic reproduction, by means of *Tetraglene* stolons, provided with 2 pairs of latero-ventral eyes.

Species and distribution. Cosmopolitan in temperate and tropical waters. *Eurysyllis ehlersi* Benham, 1927; *Eurysyllis japonicum* Imajima, 2003; *Eurysyllis pacificum* (Hartman, 1954); *Eurysyllis spicum* Kudenov & Harris, 1995; *Eurysyllis tuberculata* Ehlers, 1864.

Bibliography. San Martín (2003).

Genus ***Haplosyllides*** Augener, 1924

Haplosyllides Augener, 1924: 44.

Type-species. *Haplosyllides floridana* Augener, 1924.

Diagnosis. Body of small size with few segments. Prostomium with 3 antennae, 1 pair of eyes, and 2 palps. Palps fused to a single, anteriorly bilobed piece. Two pairs of

tentacular cirri. Antennae, tentacular, anal, and dorsal cirri smooth. Parapodial lobes conical. Ventral cirri digitiform. Few, usually only 2, thick, simple chaetae per parapodium; capillary dorsal and ventral simple chaetae absent. Pharynx with tooth, located on anterior rim; anterior margin of pharynx surrounded by crown of soft papillae and a layer of cilia; occasionally, large specimens without pharyngeal tooth. Reproduction by means of stolons.

Spcies and distribution. Only three species. The genus is only known from the Caribbean Sea and the tropical Pacific. *Haplosyllides floridana* Augener, 1924; *Haplosyllides aberrans* Fauvel, 1939; *Haplosyllides ophiocomae* Martin, Britayev & Aguado (submitted).

Bibliography. San Martín, *et al.* (1997); Martin *et al.* (submitted).

Genus ***Haplosyllis*** Langerhans, 1879

Syllis (Haplosyllis) Langehans, 1879: 527.

Hemisyllis Verrill, 1900

Type-species. *Syllis spongicola* Grube, 1855.

Diagnosis. Body of small to large size (0.5- 60 mm in length) with numerous segments. Prostomium with 3 antennae, 2 pair of eyes, and 2 palps. Palps basally fused. Two pairs of tentacular cirri. Antennae, tentacular, anal, and dorsal cirri articulated. Few (1-3) slender, simple chaetae per parapodium. Ventral cirri digitiform. Pharynx with tooth, located on anterior rim; anterior margin of pharynx surrounded by crown of soft papillae.Reproduction by means of stolons.

Species and distribution. The genus is cosmopolitan. Associated with sponges and other benthic invertebrates. *Haplosyllis agelas* Uebelacker, 1982; *Haplosyllis anthogorgicola* Utinomi, 1956; *Haplosyllis basticola* Sardá & Ávila, 2002; *Haplosyllis carmenbritoae* Lattig, San Martín & Martín, 2007; *Haplosyllis cephalata* Verrill, 1900; *Haplosyllis chamaeleon* Laubier, 1960; *Haplosyllis crassicirrata* Aguado, San Martín & Nishi, 2006; (?) *Haplosyllis cratericola* (Buzhinskaja, 1980); *Haplosyllis djiboutiensis* Gravier, 1900; *Haplosyllis gula* Treadwell, 1924; ; (?) *Haplosyllis hamata* (Claparède, 1868); *Haplosyllis loboi* Paola, San Martin & Martin 2006; *Haplosyllis palpata* Verrill, 1900; *Haplosyllis spongicola* (Grube, 1855); *Haplosyllis uncinigera* (Grube, 1878); *Haplosyllis trifalcata* (Day, 1960); *Haplosyllis villogorgicola* Martin, Núñez, Riera & Gil, 2002.

Bibliography. Okada (1937); Wissocq (1966); Martín *et al.* (2002, 2003); Lattig *et al.* (2007).

Genus ***Inermosyllis*** San Martín, 2003

Inermosyllis San Martín, 2003: 326.

Pseudosyllides Augener, 1927.

Type-species. *Pseudosyllides curacaoensis* Augener, 1927.

Diagnosis. Body of medium to large size, cylindrical, ventrally flattened. Prostomium with two pairs of eyes, three antennae, and two palps. Palps fused at bases, divergent distally. Tentacular segment distinct. Two pairs of tentacular cirri. Dorsal and ventral cirri on all parapodia. Antennae, tentacular and dorsal cirri moniliform, or indistinctly articulated basally on some species. Compound chaetae with falcigerous blades, and also capillary dorsal and ventral simple chaetae on some parapodia. Pharynx unarmed, opening surrounded by crown of soft papillae. Reproduction unknown, probably by means of stolons.

Remarks. This genus is identical to *Syllis*, but lacking pharyngeal tooth.

Species and distribution. The genus is known on some tropical areas and the Mediterranean Sea. *Inermosyllis curacaoensis* (Augener, 1927); *Inermosyllis balearica* (San Martín, 1982), *Inermosyllis mexicana* (Góngora-Garza & de León-González, 1993); *Inermosyllis pseudohaploides* San Martín, Hutchings & Aguado, in press.

Bibliography. San Martín (2003).

Genus ***Karroonsyllis*** San Martín & López, 2003

Karroonsyllis San Martín & López, 2003: 192.

Type-species. *Karroonsyllis exogoneformis* San Martín & López, 2003.

Diagnosis. Body of meiofaunal size, slender, cylindrical, with numerous segments. Prostomium with two pairs of eyes and pair of anterior ocular spots; three articulated antennae. Palps long and broad, fused all along their length, except for terminal notch. Tentacular segment similar to following ones, with single pair of articulated tentacular cirri; nuchal organs as ciliated grooves inserted in ventro-lateral position. Segments without ciliary bands. Dorsal cirri on all segments, articulated, with few articles. Parapodia each with several compound chaetae, and simple dorsal and ventral capillary chaetae on posterior parapodia. Two anal cirri, similar to dorsal cirri. Pharynx with single dorsal, conical tooth and crown of soft papillae, beginning on segments 4-5.

Bibliography. San Martín & López (2003).

Genus ***Megasyllis*** San Martín, Hutchings & Aguado, submitted

Megasyllis San Martín, Hutchings & Aguado, submitted

Type-species. *Syllis corruscans* Haswell, 1886.

Diagnosis. Body of large size (greater than 30 mm), cylindrical, with numerous bi- or tri- articulated segments (sometimes more annuli per segment). Prostomium with 4 eyes, 3 antennae, 2 palps; and 2 prostomial lobes or cheeks. Palps fused basally, ventrally directed. Antennae, tentacular, anal and dorsal cirri apparently unarticulated, rough in appearance, indistinctly articulated under detailed examination, more distinctly articulated in juveniles, smoother on large specimens. Dorsal cirri originating at different levels, those more dorsal, longer than those arising more ventrally. Cirrophores distinct. Parapodia with prechaetal lobes. Ventral cirri triangular. Aciculae straight, sometimes protruding from parapodia. Compound heterogomph chaetae with two kinds of blades; few dorsal chaetae with slender, elongated blades, and numerous chaetae with shorter, larger blades with dorso-ventral gradation in size. Capillary dorsal and ventral simple chaetae present on posterior parapodia. Pharynx shorter than proventricle or almost equal in length, with an anterior tooth, surrounded by crown of numerous (around 15 or more) soft papillae. Two anal cirri. Reproduction by means of stolons.

Species and distribution. The genus is known only from Australia and Japan. *Megasyllis corruscans* (Haswell, 1885); *Megasyllis heterosetosa* (Hartmann-Schröder, 1991); *Megasyllis inflata* (Marenzeller, 1879); *Megasyllis multiannulata* Aguado & san Martín, submitted.

Bibliography. San Martín, Hutchings & Aguado (submitted a).

Genus ***Nuchalosyllis*** Rullier & Amoureux, 1979

Nuchalosyllis Rullier & Amoureux, 1979: 164.

Type species. *Nuchalosyllis lamellicornis* Rullier & Amoureux, 1979.

Diagnosis. Body long, ribbon shaped, with numerous segments. Prostomium with two pairs of eyes and three antennae anteriorly located. Palps triangular, fused at base. Two pairs of tentacular cirri. Antennae, tentacular, dorsal and anal cirri distinctly articulated. A pair of prominent nuchal epaulettes, with several transversal lamellae. Parapodia conical, with enlarged, triangular prechaetal lobes. Ventral cirri conical, exceeding

parapodial lobe. Compound chaetae, heterogomph falcigers. Reproduction by schizogamy.

Species and distribution. Only the type-species, from Brazil.

Bibliography. Rullier & Amoureux (1979); Aguado & San Martín (in press).

Genus ***Opisthosyllis*** 1879

Opisthosyllis Langerhans, 1879: 541.

Type-species. *Opisthosyllis brunnea* Langerhans, 1879

Diagnosis. Body of medium to large size (5->10 mm in length) with numerous segments. Prostomium with 3 antennae, 2 pairs of eyes and sometimes 1 pair of eyespots, and 2 palps. Palps basally fused. Two pairs of tentacular cirri; some species with an occipital flap, differentiated from first chaetiger. Antennae, tentacular, anal, and dorsal cirri distinctly articulated. Compound chaetae with falcigerous blades; capillary dorsal and ventral simple chaetae present. Ventral cirri ovate. Pharynx with tooth, located posterior to anterior rim, typically inserted behind middle of pharynx; anterior margin of pharynx surrounded by crown of soft papillae. Reproduction by means of stolons.

Species and distribution. The genus is circuntropical. *Opisthosyllis arboricola* Hartmann-Schröder, 1959; *Opisthosyllis brunnea* Langerhans, 1879; *Opisthosyllis corallicola* Hartmann-Schröder, 1965; *Opisthosyllis convexa* Lee & Rho, 1994; *Opisthosyllis japonica* Imajima, 1966; *Opisthosylis laevis* Day, 1957; *Opisthosyllis leslieharrisae* Aguado, San Martín & Nygren, 2005; *Opisthosyllis longicirrata* Monro, 1939; *Opisthosyllis longidentata* San Martín, 1991; *Opisthosyllis nuchalis* Verrill, 1900; *Opisthosyllis ankylochata* Fauvel, 1921; *Opisthosyllis simpliseta* Hartmann-Schröder, 1981; *Opisthosyllis salina* (Hartmann-Schröder, 1959); *Opisthosyllis viridis* Langerhans, 1879; *Opisthosyllis flaccida* (Grube, 1878); *Opisthosyllis mariae* Aguado, San Martín & Ten Hove (in press).

Bibliography. Aguado *et al.* (2005).

Genus ***Parahaplosyllis*** Hartmann-Schröder, 1990

Parahaplosyllis Hartmann-Schröder, 1990: 45.

Type-species. *Parahaplosyllis brevicirra* Hartmann-Schröder, 1990.

Diagnosis. Body of medium size, with numerous segments, dorso-ventrally flattened. Prostomium proportionally large, with 2 pairs of eyes, and a pair of eyespots, 3

antennae, and 2 palps. Antennae inserted on anterior margin of prostomium. Palps short, free to each other. Tentacular segment dorsally reduced; 2 pairs of tentacular cirri. Antennae, tentacular cirri and dorsal cirri short, rough, indistinctly articulated, similar in length to parapodial lobes. Ventral cirri oval. Chaetae reduced to a single dorsal capillary chaeta and a thick, hooked simple chaeta, distally bidentate, with a curved spur. Pharynx long and slender, with a curvature, with an anterior tooth and a trepan. Reproduction by means of stolons.

Species and distribution. *Parahaplosyllis brevicirra* Hartmann-Schröder, 1990.

Bibliography. Hartmann-Schröder (1990).

Genus ***Paraopisthosyllis*** Hartmann-Schröder, 1991

Paraopisthosyllis Hartmann-Schröder, 1991: 27.

Type species. *Opisthosyllis brevicirra* Hartmann-Schröder, 1979.

Diagnosis. Body robust, cylindrical, broad anteriorly, tapered posteriorly, with many segments. Dorsal and ventral surfaces covered with numerous, small papillae. Prostomium with 4 lensed eyes and 3 antennae. Palps broad, fused at base, ventrally folded. Peristomium shorter than subsequent segments, sometimes covered dorsally by chaetiger 1; 2 pairs of tentacular cirri. Nuchal organs as 2 ciliated grooves between prostomium and peristomium. Dorsal and ventral cirri on all chaetigerous segments. Antennae, tentacular, anal and dorsal cirri smooth, enlarged, club-shaped to foliaceous. Dorsal cirri usually provided with distinct cirrophores. Dorsal cirri of anterior segments alternating in size between large and small ones on some species, larger cirri arising more dorsally. Parapodia with compound, heterogomph chaetae, and dorsal and ventral simple chaetae on posterior parapodia. Pharynx wide, with pharyngeal tooth inserted far from anterior rim. Proventricle wide, voluminous. Pygidium small, with 2 anal cirri.

Remarks. Hartmann-Schröder (1979) and later San Martín & Hutchings (2006) considered this genus as a member of the subfamily Eusyllinae. However, is proposed herein as a Syllinae member (according to Aguado & San Martín, in prep.), althougth its reproduction is unknown and this adscription is not definitive.

Species and distribution. The genus is known only from Australia. *Paraopisthosyllis alternocirra* San Martín & Hutchings (2006); *Paraopisthosyllis brevicirra* (Hartmann-Schröder, 1979); *Paraopisthosyllis ornaticirra* San Martín & Hutchings, 2006; *Paraopisthosyllis phyllocirra* Hartmann-Schröder, 1991.

Bibliography. San Martín & Hutchings (2006).

Genus ***Parasphaerosyllis*** Monro, 1937

Parasphaerosyllis Monro, 1937: 273.

Type-species: *Parasphaerosyllis indica* Monro, 1937.

Diagnosis. Body of medium to large size, with numerous segments. Prostomium with 3 antennae, 2 pairs of eyes sometimes 1 pair, and 2 palps. Palps fused basally. Two pairs of tentacular cirri. Antennae, tentacular, anal, and anterior dorsal cirri distinctly articulated, from mid-body, alternating long strongly articulated dorsal cirri with short, lemon-shaped cirri, with single, inflated article. Pharynx with tooth, located on anterior rim, surrounded by crown of soft papillae. Compound chaetae with falcigerous blades; capillary dorsal and ventral simple chaetae present. Ventral cirri ovate. Schizogamic reproduction by means of stolons.

Species and distribution. The genus is circuntropical. *Parasphaerosyllis ezoensis* Imajima & Hartman, 1964; *Parasphaerosyllis indica* Monro, 1937; *Parasphaerosyllis malimali* Capa, San Martín & López, 2001; *Parasphaerosyllis uschakovi* (Chlebovitsch, 1959).

Bibliography. Monro (1937); Imajima (1966b); Westheide (1974); Capa *et al.*, 2001; .

Genus ***Plakosyllis*** Hartmann-Schröder, 1956

Plakosyllis Hartmann-Schröder, 1956: 87.

Type-species. *Plakosyllis brevipes* Hartmann-Schröder, 1956.

Diagnosis. Body small, oval, elongated, dorso-ventrally flattened. Prostomium with 2 pairs of eyes, 3 antennae and 2 spherical palps. Antennae inserted on anterior margin of prostomium; palps inserted ventrally, not fused. Dorsum without tubercles. Two pairs of tentacular cirri. Antennae, tentacular and dorsal cirri reduced to single spherical article. Ventral cirri triangular, with numerous minute pores. Two anal cirri similar to dorsal cirri. Compound chaetae with short falcigers. Pharynx with anterior dorsal tooth, surrounded by crown of about 10 soft papillae. Proventricle short. Schizogamic reproduction by means of *Tetraglene* stolons provided with 2 pairs of eyes inserted ventro-laterally. (For illustration of *Tetraglene* stolons which lack antennae; see San Martín (2003, fig. 4D) for those of *Plakosyllis brevipes*).

Species and distribution. Cosmopolitan in temperate and tropical waters. *Plakosyllis brevipes* Hartmann-Schröder, 1956; *Plakosyllis quadrioculata* Perkins, 1981.

Bibliography. Hartmann-Schröder (1956); Gidholm (1967); San Martín (2003); San Martín *et al.* (in press).

Genus ***Rhopalosyllis*** Augener, 1913

Rhopalosyllis Augener, 1913: 245.

Type species: *Rhopalosyllis hamulifera* Augener, 1913.

Diagnosis. Body long, robust, cylindrical, with numerous segments; most posterior segments achaetous. Body covered with numerous, small papillae, present on prostomium, both dorsally and ventrally, parapodia and anal cirri. Prostomium with 4 eyes and 3 antennae. Palps fused at bases, rounded, sometimes ventrally folded. Peristomium dorsally reduced, with 2 pairs of tentacular cirri. Nuchal organs as 2 ciliated grooves between prostomium and peristomium. Dorsal and ventral cirri present on all parapodia. Antennae, tentacular and dorsal cirri obscurely articulated, short, oval to spindle-shaped, rough, covered by papillae. Ventral cirri conical. Compound chaetae heterogomph; on posterior segments some chaetae with fused shafts and blades, forming thick, bidentate hooks; dorsal and ventral simple chaetae present on most posterior parapodia. Pharynx and proventricle short; pharyngeal tooth long and slender. Reproduction by stolons.

Species and distribution. Only the type-species, from Western Australia.

Bibliography. Augener (1913); San Martín *et al.* (in press).

Genus ***Syllis*** Lamarck, 1818

Syllis Lamarck, 1818: 318.

Lalage F. Müller, 1858

Trichosyllis Schmarda, 1861

Isosyllis Ehlers, 1864

Pagenstecheria Quatrefages, 1865

Thoe Kinberg, 1866

Ioida Johnston, 1840

Aporosyllis Quatrefages, 1865

Langerhansia Czerniavsky, 1881

Reductotyposyllis Hartmann-Schröder, 1974

Type-species. *Syllis monilaris* Lamark, 1818.

Diagnosis. Body of medium to large size (5->10 mm in length) with numerous segments. Prostomium with 3 antennae, 2 pairs of eyes and sometimes 1 pair of eyespots, and 2 palps. Palps basally fused. Two pairs of tentacular cirri. Antennae, tentacular, anal, and dorsal cirri distinctly articulated. Pharynx with tooth, located on anterior rim or slightly back; anterior margin of pharynx surrounded by crown of soft papillae. Compound chaetae with falcigerous blades; capillary dorsal and ventral simple chaetae present. Ventral cirri ovate. Reproduction by means of stolons.

Species and distribution. The genus is cosmopolitan. *Syllis aciculata* (Treadwell, 1919); *Syllis aciculigrossa* (San Martín, 1990); *Syllis adamanteus* (TreadwellL, 1914); *Syllis alosae* San Martín, 1992; *Syllis Syllis albanyensis* (Hartmann-Schröder, 1984); *Syllis alternata* Moore, 1908; *Syllis amica* Quatrefages, 1866; *Syllis anoculata* (Hartmann-Schröder, 1962); *anops* Ehlers, 1897; *Syllis antarctica* (Averincev, 1972); *Syllis armillaris* O.F. Müller, 1776; *Syllis barbata* San Martín, 1992; *Syllis bella* Chamberlin, 1919; *Syllis beneliahuae* (Campoy & Alquézar, 1982); *Syllis bifida* (Hartmann-Schröder, 1986); *Syllis botosaneanui* (Hartmann-Schröder, 1973); *Syllis broomensis* (Hartmann-Schröder, 1979); *Syllis busseltonensis* (Hartmann-Schröder, 1982); *Syllis benguellana* Day, 1963; *Syllis bifurcata* (Hartmann-Schröder, 1980); *Syllis brasiliensis* McIntosh, 1885; *Syllis brevicirrata* McIntosh,1908; *Syllis brevicirris* Hansen, 1882; *Syllis caeca* (Katzmann, 1973); *Syllis castroviejoi* Capa, San Martín & López, 2001; *Syllis cerina* Grube, 1878; *Syllis compacta* Gravier, 1906; *Syllis corallicola* Verrill, 1900; *Syllis cornuta* Rathke, 1843; *Syllis crassicirrata* (Treadwell), 1925; *Syllis cruzi* Nuñez & San Martín, 1991; *Syllis curticirris* (Hartmann-Schröder, 1981); *Syllis dayi* (Hartmann-Schröder, 1974); *Syllis danieli* San Martín, 1992; *Syllis dentata* (Hartmann-Schröder, 1960); *Syllis edensis* (Hartmann-Schröder, 1989); *Syllis ehlersioides* (Marenzeller, 1890); *Syllis ergeni* Çinar, 2005; *Syllis elongata* (Johnson, 1901); *Syllis erikae* (Hartmann-Schröder, 1981); *Syllis farallonensis* (Blake & Walton, 1977); *Syllis fasciata* Malmgren, 1867; *Syllis ferrani* Alós & San Martín, 1987; *Syllis filidentata* (Hartmann-Schröder, 1962); *Syllis garciai* (Campoy, 1982); *Syllis gerlachi* (Hartmann-Schröder, 1960); *Syllis gerundensis* (Alós & Campoy, 1981); *Syllis glandulata* Nogueira & San Martín, 2002; *Syllis glarearia* (Westheide, 1974); *Syllis gracilis* Grube, 1840; *Syllis hawaiiensis* (Hartmann-Schröder, 1965); *Syllis heronislandensis* (Hartmann-Schröder,1991); *Syllis heterocirrata* (Hartmann-Schröder, 1960); *Syllis heterochaeta* Moore, 1909; *Syllis hyalina* Grube, 1863; *Syllis hyllebergi* (Licher, 1999); *Syllis hyperioni* Dorsey & Phillips, 1987; *Syllis horrocksensis*

(Hartmann-Schröder, 1981); *Syllis japonica* (Imajima, 1966); *Syllis kabilica* (Ben-Eliahu, 1977); *Syllis kerguelensis* (Averincev, 1972); *Syllis komodoensi*s Aguado, San Martín & Ten Hove (in press); *Syllis krohni* Ehlers, 1864; *Syllis licheri* Ravara, San Martín & Moreira; 2004; *Syllis longissima* Gravier, 1900; *Syllis longosegmentata* Grube, 1857; *Syllis lunaris* (Imajima, 1966); *Syllis lutea* (Hartmann-Schröder, 1960); *Syllis luteoides* (Hartmann-Schröder, 1962); *Syllis macrodentata* (Hartmann-Schröder, 1982); *Syllis magdalena* Wesenberg-Lund, 1962; *Syllis magellanica* Augener, 1918; *Syllis magna* (Westheide, 1974); *Syllis magnipectinis* Storch, 1967; *Syllis marugani* Aguado & San Martín, 2006; *Syllis maryae* San Martín, 1992; *Syllis mauretanica* (Licher, 1999); *Syllis mayeri* Musco & Giangrande, 2005; *Syllis mexicana* (Rioja, 1960); *Syllis microoculata* (Hartmann-Schröder, 1965); *Syllis monilaris* Savigny, 1812; *Syllis monilata* (Imajima, 1966); *Syllis neglecta* Grube, 1870; *Syllis nidrosiensis* Bidenkap, 1907; *Syllis nigrescens* Grube, 1878; *Syllis nigricirris* Grube, 1863; *Syllis nuchalis* (Hartmann-Schröder, 1960); *Syllis okadai* Fauvel, 1934; *Syllis onkylochaeta* Hartmann-Schröder, 199l; *Syllis ortizi* San Martín, 1992; *Sylis papillosus* (Tovar-Hernández, Granados-Barba & Solís-Weiss, 2002); *Syllis parateinopterona* (Hartman & Fauchald, 1971); *Syllis parturiens* (Haswell,1920); *Syllis patriciae* (Hartmann-Schröder, 1981); *Syllis pectinans* Haswell, 1920; *Syllis pharobroomensis* (Hartmann-Schröder, 1979); *Syllis pharynxcircumfusata* (Hartmann-Schröder, 1979); *Syllis pigmentata* (Chamberlin, 1919); *Syllis pilosa* Aguado & San Martín, submitted; *Syllis prolifera* Krohn, 1852; *Syllis prolixa* Ehlers, 1901; *Syllis pseudoarmillaris* Nogueira & San Martín, 2002; *Syllis pulvinata* (Langerhans, 1881); *Syllis ramosa* McIntosh, 1879; *Syllis raygeorgei* (Hartmann-Schröder, 1979); *Syllis remanei* (Hartmann-Schröder, 1960); *Syllis riojai* (San Martín, 1990); *Syllis robertianae* McIntosh,1885;*Syllis rosea* (Langerhans, 1879); *Syllis rubicunda* Aguado & San Martín, submitted; *Syllis sclerolaema* Ehlers, 1901; *Syllis schulzi* (Hartmann-Schröder, 1960); *Syllis setoensis* (Imajima, 1966); *Syllis silkeae* (Licher, 1999); *Syllis sol* San Martín, 2004; *Syllis spongiphilla* Verrill, 1886;*Syllis stellaepolaris* (Hartmann-Schröder, 1993); *Syllis taiwanensis* (Licher, 1999); *Syllis tegulum* (Hartman & Fauchald, 1971); *Syllis torquata* Marion & Bobretzky, 1875; *Syllis tyrrhena* (Licher & Kuper, 1998); *Syllis truncata* Haswell, 1920; *Syllis typica* (Moore, 1909); *Syllis umbricolor* Grube, 1878; *Syllis valida* Grube, 1857; *Syllis variegata* Grube, 1860; *Syllis villenai* Aguado, San Martín & Ten Hove (in press); *Syllis violacea* Grube, 1870; *Syllis vittata* Grube, 1840; *Syllis vivipara* Krohn, 1869; *Syllis warrnamboolensis* (Hartmann-Schröder, 1987); *Syllis westheidei*

San Martín, 1984; *Syllis yallingupensis* (Hartmann-Schröder, 1982); *Syllis ypsyloides* Aguado, San Martín & Ten Hove (in press).

Bibliography. Potts (1911); Okada (1937); Durchon (1959); Franke (1980, 1983, 1986, 1999); Licher (1999); San Martín (1992; 2003).

Genus ***Tetrapalpia*** San Martín, Hutchings & Aguado, in press

Tetrapalpia San Martín, Hutchings & Aguado, in press.

Type-species. *Opisthosyllis dorsoaciculata* Hartmann-Schröder, 1991.

Diagnosis. Body of medium size, dorsally cylindrical, with numerous segments. Prostomium with 4 eyes and sometimes a pair of eyespots, 3 antennae and 2 palps. Palps free, with distinct gap between them; each palp bilobed with lobes fused for most of their length. Two pairs of tentacular cirri. Antennae, tentacular, anal, and dorsal cirri distinctly articulated. Parapodia bi-lobed. Ventral cirri triangular. Compound chaetae with short falcigerous blades; capillary chaetae present. Pharynx shorter than proventricle; tooth inserted just behind slightly back from anterior margin of pharynx. Reproduction by means of stolons.

Remarks. The type species was originally assigned to the genus *Opisthosyllis*, however this species differs in several characters to other species within this genus; such as the position of the pharyngeal tooth which is located just behind the opening of the pharynx, a shorter pharynx and palps free to their bases, bilobed, with the lobes fused for most of their length; so that it appears that four palps are present.

Species and distribution. Only the type-species, from Australia.

Bibliography. Hartmann-Schröder (1991); San Martín, Hutchings & Aguado (in press).

Genus ***Trypanoseta*** (Imajima & Hartman, 1964)

Trypanosyllis (Trypanoseta) Imajima & Hartman, 1964: 129.

Geminosyllis Imajima, 1966

Type-species. *Trypanosyllis (Trypanoseta) ohma* Imajima & Hartman, 1964.

Diagnosis. Body of medium to small size (5->10 mm in length) with numerous segments. Prostomium with 3 antennae, 2 pair of eyes, and 2 palps. Palps basally fused. Two pairs of tentacular cirri. Antennae, tentacular, anal, and dorsal cirri articulated. Some thick, simple chaetae per parapodium. Ventral cirri digitiform. Pharynx with middorsal tooth, located on anterior rim; anterior margin of pharynx surrounded by crown of soft papillae and often a trepan. Reproduction by means of stolons.

Remarks. The genus was described with trepan, however, Aguado & San Martín (submitted) found a specimen of *T. ohma* without a real chitinous trepan.

Species and distribution. The genus is known from the Northern Pacific and Western Mediterranean. *Trypanoseta ohma* Imajima & Hartman, 1964; *Trypanoseta granulosa* (Lattig, San Martín & Martín, 2007).

Bibliography. Imajima & Hartman (1964); Imajima (1966c); Lattig *et al.* (2007); Aguado *et al.* (submitted).

Genus ***Trypanosyllis*** Claparède, 1864

Trypanosyllis Claparède, 1864: 558

Tetraglene Grube, 1863

? *Eurymedusa* Kinberg, 1866

Parapterosyllis Hartmann-Schröder, 1960

Trypanedenta Imajima & Hartman, 1964

Parautolytus Pillai, 1965

Pseudosyllis Grube, 1863

Type-species. *Syllis zebra* Claparède, 1864.

Diagnosis. Body of medium to large size, ribbon-like, dorso-ventrally flattened, with numerous short segments. Dorsum with transverse bands of minute spinose papillae on some species, only distinct under SEM. Prostomium with 4 eyes and 3 antennae. Palps completely free. Two pairs of tentacular cirri. Antennae, tentacular and dorsal cirri articulated. Pharynx provided with a trepan, with or without mid-dorsal tooth. Most of species with compound chaetae with falcigerous blades, and simple dorsal and ventral capillary chaetae. In some few species (subgenus *Trypanobia*) only few simple chaetae by blades and shafts fussion. Pygidium with 2 articulated anal cirri. Reproduction by means of *Tetraglene* stolons. Some species with a special kind of gemmiparity, consisting in the development of numerous stolons forming a cluster.

Remarks. The subgenus *Trypanobia* was erected by Imajima & Hartman (1964) to differentiate a group of species with only simple chaetae. These species need to be checked in order to determine if they are members of *Trypanosyllis* or they might be considered another different genus.

Species and distribution. The genus is cosmopolitan. *Trypanosyllis adamanteus* Treadwell, 1914; *Trypanosyllis aeolis* Langerhans, 1879; *Trypanosyllis coeliaca* Claparède, 1868; *Trypanosyllis gemmipara* Johnson, 1901; *Trypanosyllis gigantea*

(McIntosh, 1885); *Trypanosyllis ingens* Johnston, 1902; *Trypanosyllis inglei* Perkins, 1981; *Trypanosyllis intermedia* Moore, 1909; *Trypanosyllis parazebra* Hartmann-Schröder, 1965; *Trypanosyllis parvidentata* Perkins, 1981; *Trypanosyllis prampramensis* Augerner, 1918; *Trypanosyllis sanmartini* Çinar, 2007; *Trypanosyllis savagei* Perkins, 1981; *Trypanosyllis zebra* (Grube, 1860); (?) *Trypanosyllis* (*Trypanobia*) *depressa* Augener, 1913; (?) *Trypanosyllis* (*Trypanobia*) *asterobia* Okada, 1933; (?) *Trypanosyllis* (*Trypanobia*) *dollfusi* Fauvel, 1933.

Bibliography. Potts (1911, 1913); Okada (1937); Durchon (1957); Imajima & Hartman (1964); Imajima (1966b); San Martín (2003); Çinar (2007).

Genus ***Xenosyllis*** Marion & Bobretzky, 1875

Xenosyllis Marion & Bobretzky, 1875: 26.

Type-species: *Syllis scabra* Ehlers, 1864.

Diagnosis. Body of medium size, elongated, dorso-ventrally flattened, convex dorsally, with numerous, short segments. Prostomium with 4 eyes, 3 antennae and 2 palps. Palps free from each other, ventrally located. Prostomium and lateral margins of each segment with papillae; dorsally provided with longitudinal striations. Tentacular segment reduced, dorsally covered by small lobe with papillae. Antennae, tentacular, anal, and dorsal cirri short, articulated, covered by papillae. Compound chaetae with falcigerous blades and capillary simple chaetae. Pharynx long, unarmed. Proventricle short. Two anal cirri.

Species and distribution. The genus is known from N Atlantic and Australia. *Xenosyllis moloch* San Martín, Hutchings & Aguado, in press; *Xenosyllis scabra* Ehlers, 1864; *Xenosyllis scabroides* San Martín, Hutchings & Aguado, in press.

Bibliography. San Martín (2003); San Martín *et al.* (in press).

“Eusyllinae” Malaquin, 1893

Diagnosis. Body cylindrical, size from minute to large. Palps basally fused or free at bases. Three antennae, usually long, extending beyond palps. Four lensed eyes and sometimes two anterior eyespots (few genera with only two eyes). Two pairs of tentacular cirri, typically long and slender. Nuchal organs consist in two dorsolateral, densely ciliated grooves between prostomium and peristomium. Dorsal cirri typically long, slender, smooth or pseudoarticulated (few genera with short dorsal cirri).Pharynx

straight, typically with a middorsal, anterior tooth (some genera without middorsal tooth or localted posteriorly in pharynx). Reproduction by epigamy; only few genera brood eggs.

Remarks. Some genera are included momentarily within this group that lacks taxonomic rank until its possible monophyly is resolved.

Key to genera of "Eusyllinae"

1.- Pharyngeal tooth absent; pharynx with an incomplete trepan formed by few teeth, backwardly directed……*Odontosyllis*

.- Pharyngeal tooth present……..2

2.- Pharynx with middorsal tooth and an incomplete trepan of numerous small denticles, frontally directed…….……*Eusyllis*

.- Pharynx only with middorsal tooth……3

3.- Blades of compound chaetae with tendon connecting proximal tooth with margin. Pharyngeal tooth located near anterior rim, on midle of pharynx or posteriorly in midline. Palps free……...…….*Opisthodonta* (in part)

.- Blades of compound chaetae lacking such tendon……4

4.- Ventral cirri of anterior parapodia laminar, partially fused to parapodial lobes. Pharyngeal tooth located near anterior rim, on midle of pharynx or posteriorly in midline……..... *Opisthodonta* (in part)

.- Different ventral cirri ……..5

5.- Some dorsal cirri inflated, club-shaped. Pharyngeal tooth located on midle of pharynx……..*Basiodiosyllis*

.- Dorsal cirri not inflated…….……....6

6.- Pharyngeal tooth located posteriorly. Several anterior parapodia with distally inflated acicula…….…….*Streptodonta*

.- Pharyngeal tooth located anteriorly. Without inflated aciculae……..…..…….7

7.- Palps distincly long, fused basally and also fused to prostomium. Dorsal cirri of midbody short, exogonid-like; remaing appendages long…….*Palposyllis*

.- Palps distinct to prostomium. ……8

8.- Ventral cirri inserted distally on parapodial lobes. Dorsal cirri of two lengths, long and filiform and extremely short exogonid-like dorsal cirri that alternate along body……..……...*Westheidesyllis*

.- Ventral cirri inserted at bases of parapodia. Dorsal cirri similar throughout or else differences between short and long cirri not as pronounced ……...…….9

9.- Antennae, tentacular and anterior dorsal cirri articulated (adults)……..10

.- Antennae and cirri smooth, sometimes rugose, pseudoarticulated ……..…..……11

10.- Segments posterior to proventricle fused in units of 2-3 segments. Subcirral papilla absent. Palps completely free…….*Synmerosyllis*

.- Segments not fused. Small subcirral papilla present on parapodia, shorter than width of dorsal cirrus. Palps fused at base ……..……... *Paraehelersia*

11.- Dorsal cirri (except some anteriormost) exogonid-like, short, slightly longer than parapodial lobes. Ventral simple chaeta thick, acicular……..*Brevicirrosyllis*

.- Dorsal cirri long. Ventral simple chaeta capillar, slender……..12

12.- Small to minute size (< 5 mm in length). Pharynx short, shorter than proventricle, with a long tooth. Compound chaetae unidentate or provided with small, spine-like proximal tooth ……..*Nudisyllis*

.- Medium to large size (> 5 mm in length). Pharynx long. Compound chaetae bidentate. Distinct prechaetal lobe present. Acicula straight, extending beyond parapodial lobes. Blades of compound chaetae without long, fine spines; without spiniger-like chaetae. Large size, distinctly macrofaunal (> 10 mm in length)……..*Pionosyllis*

Genus ***Basidiosyllis*** San Martín, López & Aguado, submitted

Basidiosyllis San Martín, López & Aguado, submitted.

Type species. *Pionosyllis fusigera* Augener, 1913.

Diagnosis. Body slender, small, medium to meiofaunal size. Without ciliary bands. Segments fused on one piece. Prostomium provided with four eyes, three antennae and two palps. Median antenna inserted on anterior margin of prostomium. Palps fused at their bases, triangular. Nuchal organs as two ciliated grooves. Two pairs of tentacular cirri. Antennae, tentacular cirri and dorsal cirri similar in shape, smooth, club-shaped, slender at base and wider distally; some dorsal cirri inflated. Subcirral papilla absent. Compound chaetae heterogomph, provided with falcigerous bidentate blades, with both teeth similar in size or slightly different; spines on margin short. Tips of aciculae acuminate or tricuspidate. Parapodia with prechaetal lobes short, small. Pharynx and proventricle of similar size, short. Pharyngeal tooth located mid-pharynx. Reproduction unknown.

Species and distribution. All the known species live in tropical waters. *Basidiosyllis fusigera* (Augener, 1913); *Basidiosyllis kalimna* (San Martín & Hutchings, 2006); *Basidiosyllis victoriae* San Martín, López & Aguado, submitted.

Bibliography. San Martín & Hutchings (2006); San Martín *et al.* (submitted b).

Genus ***Brevicirrosyllis*** San Martín, López & Aguado, submitted.

Brevicirrosyllis San Martín, López & Aguado, submitted.

Type species. *Pionosyllis weismanni* Langerhans, 1879.

Diagnosis. Body of macrofaunal to medium size, some species filiform. Without ciliary bands. Segments not fused. Prostomium with two pairs of eyes and two anterior eyespots or without eyes, bearing three antennae and two palps; median antenna inserted near posterior margin of prostomium. Palps fused at their bases, with a dorsal furrow, divergent, triangular in shape. Peristomium with two pairs of tentacular cirri. Antennae, tentacular cirri and dorsal cirri of first chaetiger long, smooth to rugose or pseudoarticulated; when very long; remaining dorsal cirri short, exogonid-like, somewhat longer than parapodial lobes. Parapodia without prechaetal lobes. Subcirral papilla absent. Ventral cirri inserted at bases of parapodial lobes, not modified. Compound chaetae heterogomph or hemigomph bidentate falcigers, with moderately long or short bidentate blades; spines on margin short. Dorsal and ventral simple chaetae on posterior parapodia. Ventral simple chaetae enlarged, usually with proximal tooth longer than distal tooth, and provided with a hood. Tips of aciculae acuminate. Pharynx and proventricle similar in length; pharyngeal tooth located on anterior rim. Reproduction by epigamy.

Species and distribution. The genus is cosmopolitan in temperate and tropical areas. *Brevicirrosyllis ancori* (San Martín & Hutchings, 2006); *Brevicirrosyllis gorringensis* (Hartmann-Schröder, 1977); *Brevicirrosyllis mariae* (San Martín & Hutchings, 2006); *Brevicirrosyllis mayteae* (San Martín & Hutchings, 2006); *Brevicirrosyllis weismanni* (Langerhans, 1879).

Bibliography. San Martín *et al.* (submitted b).

Genus ***Eusyllis*** Malmgren, 1867

Eusyllis Malmgren, 1867: 40

? *Claparedia* Quatrefages, 1865

Desmosyllis Verrill, 1900

? *Synsyllis* Verrill, 1900

Eudontosyllis Knox, 1960

Type species: *Eusyllis blomstrandi* Malmgren, 1867.

Diagnosis. Body of medium to small size (10 to < 5 mm in length), cylindrical. Prostomium with 4 eyes and sometimes 2 anterior eyespots. Three antennae. Palps

either entirely free or fused just basally. Nuchal organs as 2 ciliated grooves, ciliation extending sometimes to prostomium and peristomium, as well as other segments. Two pairs of tentacular cirri. Antennae, tentacular and dorsal cirri non-articulated, sometimes rugose, with pseudoarticulate appearance. Compound chaetae; dorsal and ventral simple chaetae on some parapodia. Pharynx with mid-dorsal tooth, usually large and conspicuous, and incomplete crown of small denticles, anteriorly pointing. Pygidium with 2 anal cirri. Reproduction by epigamy.

Species and distribution. The genus is cosmopolitan. *Eusyllis antillensis* Augener, 1922; *Eusyllis assimilis* Marenzeller, 1875; *Eusyllis blomstrandi* Malmgren, 1867; *Eusyllis japonica* Imajima & Hartman, 1964; *Eusyllis kupfferi* Langerhans, 1879 ; *Eusyllis lamelligera* Marion & Bobretzky, 1875; *Eusyllis longocirrata* Imajima, 1966; *Eusyllis maxima* (Monro, 1930) ; *Eusyllis nuchalata* Hartmann-Schröder, 1965.

Bibliography. Malmgren (1867); Garwood (1991); San Martín (2003); San Martín & Hutchings (2006).

Genus ***Nudisyllis*** Knox & Cameron 1970

Nudisyllis Knox and Cameron, 1970: 77.

Type species. *Nudisyllis tinihekea* Knox and Cameron, 1970

Diagnosis. Body small, fragile, < 5 mm in length. Prostomium large, about width of 2 segments, with 4 eyes and sometimes pair of anterior eyespots. Three antennae. Palps separated, free from each other, sometimes adjacent at base. Median antenna inserted on middle of prostomium or anteriorly, on line with lateral antennae. Two pairs of tentacular cirri. Nuchal organs as 2 ciliated grooves between prostomium and peristomium. Dorsal cirri on all chaetigers, long, cylindrical, smooth or slightly rugose. Ventral cirri triangular. Compound chaetae with both unidentate and bidentate blades on same parapodium, or all unidentate; bidentate blades having proximal tooth small, spine-like. Tips of aciculae tricuspidate or lancet-shaped. Pharynx small, shorter than proventricle; pharyngeal tooth located near anterior rim, usually long. Pygidium with 2 anal cirri. Reproduction by epigamy, probably with dorsal incubation of eggs (reported on two species).

Species and distribution. The genus is reported on Atlantic and Pacific oceans and their adjacent seas. *Nudisyllis divaricata* (Keferstein, 1862); *Nudisyllis magnidens* (Day, 1953); *Nudisyllis pulligera* (Krohn, 1852); *Nudisyllis tinihekea* Knox and Cameron, 1970.

Bibliography. Pierantoni, 1905; Knox & Cameron (1970); San Martín & Hutchings, 2006; San Martín *et al.* (submitted b).

Genus ***Odontosyllis*** Claparède, 1863

Odontosyllis Claparède, 1863: 47.

Procome Ehlers, 1864

?*Eurymedusa* Kinberg, 1865

Parautolytus Ehlers, 1900

Fauvelia Gravier, 1900

Alluaudella Gravier, 1905

? *Hesperalia* Chamberlin, 1919

?*Atelesyllis* Pruvot, 1930

Pharyngeovalvata Day, 1951

Odontoautolytus Hartmann-Schröder, 1979

?*Synpalposyllis* Hartmann-Schröder, 1983

Umbellisyllis Sars, 1869

Type species. *Syllis fulgurans* Audouin & Milne Edwards, 1833.

Diagnosis. Body of variable size, from 5 mm to 10 mm in length, with numerous segments, cylindrical, dorsally highly convex, flattened ventrally. Prostomium with 4 eyes and, sometimes, pair of anterior eyespots. Three antennae. Palps broad, free for almost all their length, fused basally. Peristomium usually reduced dorsally; 2 pairs of tentacular cirri. Occipital flap present, usually well developed, covering peristomium dorsally and prostomium partially. Nuchal organs as 2 ciliated grooves between prostomium and peristomium, extending sometimes to lateral areas of prostomium. Dorsal cirri elongated, smooth, distally tapered, but sometimes short or indistinctly articulated. Parapodia usually with pre- and postchaetal lobes. Ventral cirri digitiform to pillow-shaped. Compound chaetae heterogomph, usually with shafts distally spinose. Dorsal and ventral simple chaetae present on some parapodia. Pharynx short, distinctly shorter than proventricle, provided with several teeth, usually few, pointing backwards, pharyngeal mid-dorsal tooth absent; pharynx when not everted situated posteriorly to chaetiger 1, inside tube that leads to mouth opening on peristomium. Proventricle usually long and wide, massive. Pygidium with 2 anal cirri. Reproduction by epigamy; epigamic specimens sometimes strongly modified and phosphorescent.

Species and distribution. The genus is cosmopolitan. *Odontosyllis annulatus* (Hartmann-Schröder, 1979); *Odontosyllis arenicolor* Grube, 1878; *Odontosyllis atypica* Chamberlin, 1919; *Odontosyllis australiensis* Hartmann-Schröder, 1979; *Odontosyllis brachyodonta* Verrill, 1900; *Odontosyllis brevipes* Hartmann-Schröder, 1959; *Odontosyllis ctenostoma* Claparède, 1868; *Odontosyllis cuculata* (McIntosh, 1908); *Odontosyllis detecta* Augener, 1913; *Odontosyllis freycinetensis* Augener, 1913; *Odontosyllis fulgurans* (Audouin & Milne Edwars, 1834); *Odontosyllis gibba* Claparède, 1863; *Odontosyllis guillermoi* Fukuda & Nogueira, 2006; *Odontosyllis globulocirrata* Hartmann-Schröder, 1981; *Odontosyllis gravelyi* Fauvel, 1930; *Odontosyllis heterodonta* Góngora-Garza & de León-González, 1993; *Odontosyllis langerhansiaesetosa* Hartmann-Schröder, 1979; *Odontosyllis lineata* Hartmann-Schröder, 1962; *Odontosyllis longicornis* Hartmann-Schröder, 1960; *Odontosyllis longigulata* Perkins, 1981; *Odontosyllis lucifera* (Verrill, 1875); *Odontosyllis luminosa* San Martín, 1990; *Odontosyllis maculata* Uschakov, 1950; *Odontosyllis magnanuchalata* Hartmann-Schröder, 1965; *Odontosyllis marombibooral* San Martín & Hutchings, 2007; *Odontosyllis micropedata* Hartmann-Schröder, 1965; *Odontosyllis multidenticulatus* (Harrtmann-Schröder, 1959); *Odontosyllis octodentata* Treadwell, 1917; *Odontosyllis parva* Berkeley, 1923; *Odontosyllis phosphorea* Moore, 1909; *Odontosyllis polycera* (Schmarda, 1861); *Odontosyllis psammocroma* Augener, 1924; *Odontosyllis rubrofasciata* Grube, 1878; *Odontosyllis setoensis* Imajima, 1966; *Odontosyllis suteri* Benham, 1915; *Odontosyllis tubicola* (Uschakov, 1950), *Odontosyllis twincayensis* Russell, 1989; *Odontosyllis undecimdonta* Imajima & Hartman, 1964.

Bibliography. Claparède (1863); Daly (1975); Fischer & Fischer, 1995; Gaston & Hall (2000); San Martín & Hutchings (2006).

Genus ***Opisthodonta*** Langerhans, 1879

Opisthodonta Langerhans, 1879: 547.

Type species. *Opisthodonta morena* Langerhans, 1879.

Diagnosis. Body long, with numerous segments, stout, dorsally convex, of macrofaunal size (> 10 mm in length). Prostomium provided with 2 pairs of eyes, and sometimes 2 anterior eyespots. Three antennae. Median antenna inserted on middle of prostomium or slightly in front of anterior eyes. Palps apparently free from each other, just basally fused. Peristomium small, partially covered by prostomium and first chaetiger, with 2

pairs of tentacular cirri. Nuchal organs as 2 ciliated grooves between prostomium and peristomium. Dorsal cirri on all chaetigers, cylindrical, long to extremely long, smooth or slightly rugose. Parapodia elongate; ventral cirri of anterior parapodia, ovate, foliaceous almost completely fused with parapodial lobe, provided with hyaline inclusions, perhaps glands. Subsequent ventral cirri conical to digitiform, neither foliaceous nor fused to parapodial lobes, inserted at base of parapodia. Chaetal bundles formed of numerous compound chaetae, including falcigers provided with long, thick proximal tooth and short distal tooth and sometimes a few chaetae with long, slender, spiniger-like blades. Dorsal simple chaetae apparently lacking. Aciculae with button-shaped tips with crown of spines, or tricuspidate. Pharynx and proventricle similar in length. Pharynx with crown of soft papillae on anterior rim and single mid-dorsal tooth, inserted on anterior third or middle of pharynx. Reproduction by epigamy.

Species and distribution. The genus is distributed worldwide, except polar seas. *Opisthodonta hanneloreae* San Martín & Hutchings, 2007; *Opisthodonta longocirrata* (Saint-Joseph, 1886); *Opisthodonta luquei* (San Martín, 1990); *Opisthodonta melaenonephra* (Haswell, 1920); *Opisthodonta mitchelli* Kudenov & Harris, 1995; *Opisthodonta morena* Langerhans, 1879; *Opisthodonta rousei* (San Martín & Hutchings, 2006); *Opisthodonta russelli* San Martín, López & Aguado, submitted; *Opisthodonta serratisetosa* (López, San Martín & Jiménez, 1987); *Opisthodonta templadoi* (San Martín, 1991); *Opisthodonta tridentata* (Kudenov & Harris, 1995); *Opisthodonta uraga* (Imajima, 1966).

Bibliography. Langerhans (1879); Hartmann-Schröder (1971); San Martín & Hutchings (2006); San Martín *et al.* (submitted b)

Genus ***Palposyllis*** Hartmann-Schröder, 1977

Palposyllis Hartmann-Schröder, 1977: 87, enmended by San Martín & Aguirrezabalaga, 1988.

Type species. *Palposyllis prosostoma* Hartmann-Schröder, 1977.

Diagnosis. Body of macrofaunal size, cylindrical, long and slender. Prostomium without eyes. Prostomium fused with palps. Three antennae. Median antenna inserted on middle of prostomium. Palps elongated, fused at bases, without dorsal furrow. Two pairs of tentacular cirri. Nuchal organs as 2 ciliated grooves between prostomium and peristomium. Antennae, tentacular cirri and dorsal cirri smooth, filiform, long anteriorly and posteriorly, shorter on midbody. Ventral cirri digitiform to filiform, elongated.

Heterogomph compound chaetae with unidentate falcigerous, short blades, with hemigomph articulations. Dorsal simple chaetae on some posterior parapodia, bidentate, with both teeth similar. Ventral simple chaeta probably absent. Parapodia without prechaetal lobes. Pharyngeal tooth anteriorly located. Reproduction unknown. Pygidium small, with 2 smooth anal cirri.

Species and distribution. Only the type-species, from deep bottoms of NE Atlantic and W Mediterranean.

Bibliography. Hartmann-Schröder (1977); San Martín & Aguirrezabalaga (1988); San Martín (2003).

Genus ***Paraehlersia*** San Martín, 2003

Paraehlersia San Martín, 2003: 61.

Type species. *Ehlersia ferrugina* Langerhans, 1881.

Diagnosis. Body long, stout, with numerous segments, adults 5 mm or greater in length, dorsally convex. Prostomium with 4 eyes and pair of anterior eyespots. Three antennae. Median antenna inserted on middle of prostomium. Palps basally fused, with dorsal furrow. Two pairs of tentacular cirri. Nuchal organs as 2 ciliated grooves between prostomium and peristomium. Antennae, tentacular cirri and anterior dorsal cirri of adults articulated to irregularly articulated depending upon size, remaining dorsal cirri smooth. Dorsal ciliary bands on segments. Parapodia without prechaetal lobes; digitiform, retractile papilla between parapodial lobes and dorsal cirri of some parapodia. Compound chaetae heterogomph, including one or more chaetae with spiniger-like blades and several bidentate falcigerous blades, anteriorly with both teeth similar, posteriorly with proximal tooth longer and more robust than distal tooth. Aciculae acuminate. Pharynx and proventricle of similar size. Pharyngeal tooth anteriorly located. Reproduction by epigamy.

Species and distribution. The genus is distributed worldwide, except on polar seas. *Paraehlersia articulata* (Kudenov & Harris, 1995); *Paraehlersia ehlersiaefiormis* (Augener, 1913); *Paraehlersia ferrugina* (Langerhans, 1881); *Paraehlersia weissmannioides* (Augner, 1913).

Bibliography. San Martín (2003); San Martín & Hutchings (2006); San Martín *et al.* (submitted b).

Genus ***Pionosyllis*** Malmgren, 1867

Pionosyllis Malmgren, 1867: 40.

Hesiosyllis Wesenberg-Lund, 1950

Type species. *Pionosyllis compacta* Malmgren, 1867 by monotypy.

Diagnosis. Body long to moderately long, stout, of macrofaunal size, dorsally strongly convex. Apparently without ciliary bands. Segments not fused. Prostomium provided with four eyes, sometimes also a pair of eyespots, with three antennae and two palps; sometimes two peristomial cheeks or lobes on large specimens. Median antenna inserted in the middle of prostomium. Palps fused at bases, with a dorsal furrow, triangular in shape. Nuchal organs as ciliated grooves. Two pairs of tentacular cirri. Antennae, tentacular cirri and dorsal cirri smooth, sometimes rugose, long, filiform, similar throughout or alternating slightly in length. Subcirral papilla absent. Ventral cirri not fused to parapodial lobes, proximally inserted; those of anteriormost parapodia inflated, more or less spherical. Heterogomph compound chaetae with bidentate falcigerous blades, the two teeth similar in size; some dorsal anterior falcigers somewhat longer than remaining in some species; other species with some unidentate blades. Dorsal and ventral simple chaeta on some posterior parapodia, bidentate, with both teeth similar; one species with filiform, unidentate dorsal simple chaeta; spines on margin of blades short to moderate. Aciculae straight, pointed, acute, usually protruding from parapodial lobes. Parapodia with prechaetal lobes. Pharynx and proventricle similar in size. Pharyngeal tooth anteriorly located. Reproduction by epigamy.

Species and distribution. The species of this genus live in polar seas and great depths of other oceans. *Pionosyllis compacta* Malmgren, 1867; *Pionosyllis enigmatica* (Wesenberg-Lund, 1950); *Pionosyllis gigantea* Moore, 1908; *Pionosyllis kerguelensis* McIntosh, 1885; *Pionosyllis magnifica* Moore, 1906; *Pionosyllis petalecirrus* Averincev, 1982; *Pionosyllis stylifera* Ehlers, 1913.

Bibliography. Malmgren (1867); San Martín & Hutchings (2006); San Martín *et al.* (submitted b).

Genus ***Streptodonta*** San Martín & Hutchings, 2006

Streptodonta San Martín & Hutchings, 2006: 353.

Type species: *Opisthodonta pterochaeta* Southern, 1914.

Diagnosis. Body long, slender, tapered anteriorly and posteriorly, with numerous segments. Prostomium pentagonal to triangular, with 4 eyes and 2 anterior eyespots.

Three antennae. Palps short, fused basally. Nuchal organs as 2 ciliated grooves between peristomium and prostomium. Two pairs of tentacular cirri. Antennae, tentacular and dorsal cirri elongated, smooth, distally tapered. Ventral cirri triangular. Compound chaetae with translucent hood on margin, ornamented with several rows of minute spines. Dorsal simple chaetae with translucent hood. Ventral simple chaetae probably absent. Aciculae of several anterior parapodia distinctly enlarged. Pharynx and proventricle long, pharyngeal tooth located laterally and distinctly posteriorly, close to proventricle. Reproduction by epigamy.

Species and distribution. Only the type-species, distributed on North Eastern Atlantic, also reported with doubts in Australia. The description of an additional species from the Arctic Ocean is currently in preparation.

Bibliography. San Martín & Hutchings (2006).

Genus ***Synmerosyllis*** San Martín, López & Aguado, submitted

Synmerosyllis San Martín, López & Aguado, submitted b

Type species. *Pionosyllis lamelligera* Saint-Joseph, 1886.

Diagnosis. Body long and slender with numerous segments, of medium size. Segments of midbody fused, forming single segments from groups of 2-3 chaetigers. Ciliary bands absent, sometimes rows of cilia on the parapodia. Prostomium provided with four eyes, sometimes also a pair of anterior eyespots, with three antennae and two palps. Median antenna inserted anteriorly, slightly back to the lateral antennae. Palps free to each other, divergent. Nuchal organs as two ciliated grooves. Two pairs of tentacular cirri. Antennae, tentacular cirri and dorsal cirri of chaetiger 1 long, weakly articulated; dorsal cirri of remaining chaetigers much shorter, smooth. Subcirral papilla absent. Ventral cirri inserted basally on parapodial lobes; ventral cirri of first chaetiger enlarged, foliaceous, laminar. Compound chaetae heterogomph falcigers with blades short to moderately long, bidentate; spines on margin short. Dorsal and ventral simple chaetae present on posterior parapodia. Tips of aciculae trifid. Parapodia without prechaetal lobes. Pharynx longer than proventricle. Pharyngeal tooth anteriorly located. Reproduction by epigamy (only demonstrated in the type species).

Species and distribution. Temperate and tropical waters. *Synmerosyllis aciculata* (San Martín, 1990); *Synmerosyllis lamelligera* (Saint-Joseph, 1886); *Synmerosyllis yolandae* (San Martín & Hutchings, 2006).

Bibliography. San Martín *et al.* (submitted b).

Genus ***Westheidesyllis*** San Martín, López & Aguado, submitted

Westheidesyllis San Martín, López & Aguado, submitted

Type species. *Eusyllis heterocirrata* Hartmann-Schröder, 1959.

Diagnosis. Body small and slender, of meiofaunal size, with dorsolateral and ventrolateral rows of cilia. Segments not fused. Prostomium with eyes or without them, with three antennae and two palps. Median antenna inserted on posterior margin of prostomium. Palps fused at their bases, with a dorsal furrow, divergent, triangular in shape. Nuchal organs as two ciliated grooves. Two pairs of tentacular cirri. Antennae, tentacular cirri and dorsal cirri long, smooth, cylindrical; short, exogonid-like, small dorsal cirri present on some parapodia of midbody. Dorsal cirri absent on chaetiger 2. Subcirral papilla absent. Ventral cirri distally inserted on parapodial lobes. Compound chaetae homogomph, with bifid articulation, provided with short falcigers, slightly bidentate, with small proximal tooth; spines of blades short to moderate. Dorsal simple chaetae on posterior parapodia; apparently without ventral simple chaetae. Tips of aciculae distally rounded or laterally expanded. Parapodia with small prechaetal lobes. Pharynx longer than proventricle or similar in size. Pharyngeal tooth anteriorly located. Reproduction unknown.

Species and distribution. Interstitial in tropical areas. *Westheidesyllis corallicola* (Ding & Westheide, 1997); *Westheidesyllis gesae* (Perkins, 1981); *Westheidesyllis heterocirrata* (Hartmann-Schröder, 1959).

Bibliography. San Martín *et al.* (submitted b).

Incertae sedis

Key to genera

1.- Nuchal epaulettes present……2

.- Nuchal epaulettes absent……..4

2.- Pharynx long, slender, coiled. Trepan present……..*Amblyosyllis*

.- Pharynx short, straight. Trepan absent……..3

3.- Dorsal cirri globular. A filiform appendage between nuchal epaulettes.....*Clavisyllis*

.- Dorsal cirri flattened. Without such filiform appendage……...*Lamellisyllis*

4.- Single pair of eyes……5

.- Two pairs of eyes, or eyes absent……..6

5.- Segments fused in several unities. Palps fused. Midbody dorsal cirri ending in 5 digitations jointed by a membrane; digitations supported by vacuoliazed cells. Pharyngeal tooth absent……*Murrindisyllis*

.- Segments not fused. Palps free. Without these digitations. Pharyngeal tooth present……..*Neopetitia*

6.- Pharynx unarmed……..7

.- Pharynx provided with tooth……8

7.- Palps fused all along their length. Antennae, tentacular cirri and anterior dorsal cirri minute, papilliform; remaining dorsal cirri long, filiform..……*Anguillosyllis*

.- Palps fused basally. Antennae, tentacular and anterior dorsal cirri long; remaining dorsal cirri short……..……...*Nooralia*

8.- Pharyngeal tooth located posteriorly. Without other denticles in pharynx……..……*Psammosyllis*

.- Pharyngeal tooth located anteriorly……..9

9.- Pharynx with an incomplete arc of denticles……...……...10

.- Pharynx without arc of denticles. Aciculae distally knobbed, with 2 unequal lobes. Blades of compound chaetae with long, fine, distally ornamented spines; sometimes with spiniger-like chaetae. Medium size (> 5 mm in length)…….*Perkinsyllis*

10.- Body minute. Dorsal cirri short……..*Miscellania*

.- Body large. Dorsal cirri very long, filiform……11

11.- Body composed by 13 chaetigers plus an achetigerous preanal segment……*Brachysyllis*

.- Body composed by numerous segments, without a preanal achaetous segment……*Dioplosyllis*

Genus ***Amblyosyllis*** Grube, 1857

Amblyosyllis Grube, 1857: 186.

Cirrosyllis Schmarda, 1861

Gattiola Johnston, 1865

Nicotia Costa, 1864

Pterosyllis Claparède, 1863

Thylaciphorus Quatrefages, 1865

Pseudosyllides Czerniavsky, 1882

Type species. *Amblyosyllis rhombeata* Grube, 1857.

Diagnosis. Body less than 5 mm in length, dorso-ventrally flattened, extremely fragile, with few segments; peristomium and last segment without parapodia and chaetae, each

with 2 pairs of cirri. Intersegmental constrictions strongly marked, midbody segments typically trapezoidal in shape. Prostomium with 3 antennae, 4 eyes, and usually 2 anterior eyespots, sometimes ventrally located. Palps short, less than length of prostomium, basally fused, divergent, usually ventrally folded, and difficult to see dorsally. Peristomium shorter than following segments, with 2 pairs of tentacular cirri, and 2 nuchal organs, forming nuchal epaulettes, usually ciliated. Antennae, tentacular and dorsal cirri long, greater than body width, usually strongly coiled, sometimes forming skeins, smooth to indistinctly articulated, fragile. Pigmentary glands on dorsal and ventral cirri, sometimes forming distinct vesicles. Pharynx long, slender, highly convoluted, with trepan formed by several teeth, lacking median tooth. Proventricle proportionally small to body width. Ventral cirri large, located latero-posteriorly to parapodial lobes, similar in length. Compound chaetae, heterogomph, bidentate falcigers, numerous, present on all chaetigers, other types of chaetae rarely present; chaetae similar in all species. Pygidium with 2 long anal cirri, third length of dorsal cirri.

Remarks. The method of reproduction is not well known. A mature male has been observed with natatory chaetae (Aguado *et al*., submitted) and one species is known to brood eggs in a gelatinous mass (Pernet, 1998). The species of this genus might be epigamic.

Species and distribution. The genus is cosmopolitan. *Amblyosyllis cincinnata* (Verrill, 1874); *Amblyosyllis enigmatica* San Martín & Hutchings, 2006; *Amblyosyllis finmarchica* (Malmgren, 1868); *Amblyosyllis formosa* (Claparède, 1863); *Amblyosyllis granosa* Ehlers, 1897; *Amblyosyllis madeirensis* Langerhans, 1879; *Amblyosyllis multidenticulata* San Martín & Hutchings, 2006; *Amblyosyllis rhombeata* Grube, 1857; *Amblyosyllis speciosa* Izuka, 1912; *Amblyosyllis vesiculosa* Hartmann-Schröder, 1989; *CirroSyllis ceylanica* Schmarda, 1861; *CirroSyllis picta* Schmarda, 1861; *CirroSyllis vittate* Schmarda, 1861; *Thylaciphorus hessii* Quatrefages, 1865.

Bibliography. Grube (1857); Pernet (1998); San Martín & Hutchings (2006).

Genus ***Anguillosyllis*** Day, 1963

Anguillosyllis Day, 1963: 400.

Braniella Hartman, 1965

Type species. *Anguillosyllis capensis* Day, 1963.

Diagnosis. Body small, meiofaunal. Prostomium with three small antennae and two palps; palps elongated, fused, with a distal notch, more or less marked. Without eyes. One pair of papilliform tentacular cirri. Antennae and tentacular cirri minute, papilliform. Dorsal cirri long, filiform, coiled over dorsum. Ventral cirri present, digitiform, inserted medially to distally. Parapodia relatively long, triangular, with a short prechaetal and elongated postchaetal lobe. Compound chaetae heterogomph, with elongated, slender blades. Pharyngeal tooth absent. Proventricle barrel-shaped

Species and distribution. All the known species of this genus live in the deep sea (183-5500 m). *Anguillosyllis capensis* Day, 1963; *Anguillosyllis palpata* (Hartman, 1967); *Anguillosyllis pupa* (Hartman, 1965).

Bibliography. Day (1963); Böggemann & Purschke (2005); Aguado & San Martín (in press).

Genus ***Brachysyllis*** Imajima & Hartman, 1964

Brachysyllis Imajima & Hartman, 1964:108.

Type species. *Brachysyllis japonica* Imajima & Hartman, 1964.

Diagnosis. Body large, macrofaunal, with 13 chaetigers plus a pre-anal achaetous segment. Segments more or less trapezoidal. Palps long, free at bases, with a subdistal small papilla. Prostomium with four eyes. Nuchal organs as ciliary rows. Rows of transversal cilia covering dorsum and ventrum. Antennae, and tentacular, anal and dorsal cirri long, filiform and smooth. Ventral cirri long, filiform, inserted proximally to parapodia. Parapodia elongate, with a triangular pre-chaetal lobe, dorsally located. Compound chaetae falcigerous, blades bidentate, dorsal and ventral simple chaetae absent. Aciculae bending distally. Pharynx wide, straight, with a large anterior dorsal tooth and an incomplete ventral arc of small denticles (5-6), surrounded by a crown of distal pharyngeal papillae. Proventricle rectangular, shorter than pharynx. Reproduction by epigamy.

Species and distribution. *Brachysyllis infuscata* (Ehlers, 1901); *Brachysyllis japonica* Imajima & Hartman, 1964; *Brachysyllis lagunae* (Hartman, 1961)

Bibliography. Imajima & Hartman (1964); Aguado & San Martín (in press).

Genus ***Clavisyllis*** Knox, 1957

Clavisyllis Knox, 1957:493.

Type species. *Clavisyllis alternata* Knox, 1957.

Diagnosis. Size macrofaunal, body long, thick. Prostomium with four eyes, three antennae and two palps. Palps fused at base, ventrally directed. Peristomium with two pairs of tentacular cirri. Two prominent, long, sinuous nuchal epaulettes, together with single, digitiform nuchal cirrus. Antennae, tentacular and dorsal cirri large, ovoid, inflated, with distinct cirrophores; ventral cirri ovoid. Compound heterogomph falcigers with blades having long spines on cutting edges. Pharynx and proventricle of similar length; anterior margin of pharynx with a mid dorsal tooth and a crown of soft papillae. Proventricle barrel-shaped.

Species and distribution. Only the type-species, from New Zealand.

Bibliography. Knox (1957); Aguado & San Martín (in press).

Genus ***Dioplosyllis*** Gidholm, 1962

Dioplosyllis Gidholm, 1962: 253.

Type species. *Dioplosyllis cirrosa* Gidholm, 1962

Diagnosis. Body long, slender, macrofaunal, with numerous chaetigers. Palps long, fused at bases. Prostomium with four eyes. Nuchal organs as ciliary rows. Rows of transversal cilia covering dorsum and ventrum. Antennae, and tentacular, anal and dorsal cirri very long, filiform and smooth. Ventral cirri digitiform, inserted subdistally to parapodia. Compound chaetae falcigerous, blades bidentate or tridentate, dorsal and ventral simple chaetae absent. Pharynx long, straight, with a large anterior dorsal tooth and an incomplete ventral arc of small denticles (5-8), surrounded by a crown of distal pharyngeal papillae. Proventricle rectangular, shorter than pharynx. Reproduction by epigamy.

Species and distribution. *Dioplosyllis cirrosa* Gidholm, 1962; *Dioplosyllis octodentata* Perkins, 1981.

Bibliography. Gidholm (1962); Mueller & Fauchald (1976); Aguado & San Martín (in press).

Genus ***Lamellisyllis*** Day, 1960

Lamellisyllis Day, 1960: 319.

Type-species. *Lamellisyllis comans* Day, 1960.

Diagnosis. A macrofaunal species, body long, thick. Prostomium with four eyes, three lamella-shaped or foliaceous antennae and two palps fused at base. Two pairs of tentacular cirri, dorsal pair foliaceous, ventral pair cirriform. Two prominent nuchal

epaulettes. Dorsal cirri large, ovoid and foliaceous, with distinct cirrophores; ventral cirri ovoid. Compound heterogomph falcigers with blades having long spines on cutting edge. Pharynx longer than proventricle. Proventricle barrel-shaped.

Species and distribution. Only the type-species, from South Africa.

Bibliography. Day (1960, 1967); Aguado & San Martín (in press).

Genus ***Miscellania*** Martin, Alós & Sardá, 1990

Miscellania Martin, Alós & Sardá, 1990: 169.

Type-species. *Miscellania dentata* Martín, Alós & Sardá, 1990

Diagnosis. Body very small, meiofaunal, with few segments. Prostomium rounded with two pairs of eyes and two anterior eyespots. Three antennae. Palps totally separated and divergent, ventrally folded. Two pairs of tentacular cirri, similar to antennae. Antennae, tentacular and dorsal cirri smooth. Dorsal cirri short, more or less fusiform. Ventral cirri short, digitiform. Compound chaetae falcigers, and dorsal and ventral capillary simple chaetae. Pharynx short, with a middorsal tooth and an incomplete arc of minute denticles. Proventricle short. Pygidium with two anal cirri.

Species and distribution. Only the type-species, from the Mediterranean Sea and near Atlantic.

Bibliography. Martin *et al.* (1990).

Genus ***Murrindisyllis*** San Martín, Aguado & Murray, 2007

Type-species. *Murrindisyllis kooromundrola* San Martín, Aguado & Murray, 2007: 40-41.

Diagnosis. Body long, slender to filiform, with up to about 50--60 chaetigers; most specimens incomplete. Body surface with transverse ciliary bands. Prostomium triangular in shape, with two eyes and 3 smooth antennae. Median antenna very long, coiled, inserted on posterior part of prostomium; lateral antennae much shorter, originating on anterior margin, latero-ventrally situated. Palps completely fused to each other and also fused to prostomium. Two pairs of tentacular cirri similar in length to lateral antennae. Antennae, tentacular and dorsal cirri smooth. Anterior segments (about 9--10) fused in single piece, including proventricular segments; midbody segments forming groups of 2 or 3 fused chaetigers. Dorsal cirri anteriorly short, longer after proventricle, very long on midbody, presenting differences in length but without a fixed alternation pattern. Dorsal cirri of midbody ending in wide expansion with five

longitudinal rows of internal vacuolated cells forming a "hand-like" structure, and joined by a membrane ("webbed"), distal end with five rounded shallow projections. Dorsal cirri of posterior parapodia short, papilliform. Ventral cirri digitiform, not projecting beyond parapodia, inserted basally. Parapodia with distal papilla. Anterior and midbody parapodia with compound, heterogomph chaetae. Blades and shafts partially fused towards posterior part of body. Posterior parapodia with simple chaetae resulting from fusion of blade with shaft. Solitary capillary dorsal and ventral chaetae on posterior parapodia. Pharynx short, unarmed, with 10 terminal papillae. Proventricle very long, about 5-7 segments. Pygidium with two long anal cirri.

Species and distribution. Only the type-species, from Australia.

Bibliography. San Martín *et al.* (2007).

Genus ***Neopetitia*** San Martín, 2003

Neopetitia San Martín, 2003: 49.

Petitia Siewing, 1956

Diagnosis. Body very small, meiofaunal, with few segments. Prostomium with single pair of eyes. Three antennae. Palps totally separated, biarticulated in appearance. Two pairs of tentacular cirri, similar to antennae. Antennae, tentacular and first pair of dorsal cirri smooth, elongated; remaining dorsal cirri short, papilliform. Ventral cirri short, digitiform, inserted subdistally in parapodial lobes. Compound chaetae falcigers, and dorsal and ventral capillary simple chaetae. Pharynx short, with a middorsal tooth. Proventricle short. Pygidium with two anal cirri and a thick medial papilla.

Species and distribution. Intertidal species in temperate and tropical waters. *Neopetitia amphophthalma* (Siewing, 1956); *Neopetitia occulta* (Westheide & Hass-cordes, 2001); *Neopetitia abadensis* Riera, Núñez & Brito, 2007.

Bibliography. Siewing (1956); Bührmann *et al.* (1996a, 1996b); Westheide & Hass-Cordes, 2001; San Martín (2003); Riera *et al.* (2007).

Genus ***Nooralia*** San Martín, 2002

Nooralia San Martín, 2002: 333.

Type-species. *Nooralia bulgannabooyanga* San Martín, 2002.

Diagnosis. Body small, short, with about 30 chaetigers. Surface of body smooth. Prostomium with 4 eyes and 3 antennae. Palps fused at bases. Two pairs of tentacular cirri. Antennae, tentacular cirri and dorsal cirri of chaetiger 1 long, cylindrical to

spindle-shaped; remaining dorsal cirri short, lanceolate. Parapodia with dorsal simple capillary chaetae and compound chaetae with unidentate and bidentate short blades. Ventral simple chaetae apparently absent. Pharynx long, unarmed, with a crown of soft papillae on anterior rim. Proventricle small, difficult to see. Pygidium with 2 large anal cirri. Females brooding eggs dorsally, by means of compound notochaetae.

Species and distribution. Only the type-species, from Australia.

Bibliography. San Martín (2002, 2005).

Genus ***Perkinsyllis*** San Martín, López & Aguado, submitted.

Perkinsyllis San Martín, López & Aguado, submitted.

Type species. *Pionosyllis longisetosa* Hartmann-Schröder, 1965.

Diagnosis. Body long and slender, of medium size to meiofaunal. Segments not fused. Anterior segments with a single dorsal row of cilia, double after proventricular segments. Prostomium with four eyes and two anterior eyespots or without eyes, with three antennae and two palps. Nuchal organs as two ciliated grooves. Median antenna inserted on middle of prostomium or on posterior margin. Palps fused at bases, with a dorsal furrow, triangular in shape. Two pairs of tentacular cirri. Antennae, tentacular and dorsal cirri long to very long, slender, thread-like, all similar, sometimes coiled over dorsum. Subcirral papilla absent. Two kinds of heterogomph compound chaetae, one provided with slender and spiniger-like, sometimes with very long blades, the other with shorter, elongate falcigers provided with long, fine, distally dressed spines on margin; some species having short spiniger-like blades or lacking. Dorsal and ventral simple chaetae on posterior parapodia**.** Aciculae distally expanded, bilobed. Parapodia without prechaetal lobes, or with very small ones. Pharynx and proventricle similar in size, or pharynx longer than proventricle. Pharyngeal tooth anteriorly located. Reproduction unknown on most species; one specimen of *P. hartmannschroederae* had attached eggs, ventrally brooded, similar brooding mode has been reported for *P. augeneri*; perhaps all species of *Perkinsyllis* brood eggs.

Species and distribution. The genus is cosmopolitan in temperate and tropical waters. *Perkinsyllis anophthalma* (Capaccioni & San Martín, 1989); *Perkinsyllis augeneri* (Hartmann-Schröder, 1979); *Perkinsyllis hartmannschroederae* (San Martín & Hutchings, 2006); *Perkinsyllis homocirrata* (Hartmann-Schröder, 1958); *Perkinsyllis longisetosa* (Hartmann-Schröder, 1965); *Perkinsyllis serrata* (Hartmann-Schröder, 1984); *Perkinsyllis spinisetosa* (San Martín, 1990).

Bibliography. San Martín & Hutchings (2006); San Martín *et al.* (submitted b).

Genus ***Psammosyllis*** Westheide, 1990

Psammosyllis Westheide, 1990: 165.

Type-species: *Psammosyllis aliceae* Westheide, 1990.

Diagnosis. Body small, of meiofaunal size, with few segments. Prostomium with 4 eyes, and 3 short antennae. Palps fused entire length or just leaving distal notch. Nuchal organs as 2 ciliated grooves between prostomium and peristomium. Two pairs of tentacular cirri. Dorsal cirri on all segments, smooth, cylindrical, longer than parapodial lobes, shorter than body width. Ventral cirri digitiform, short. Parapodial lobes bilobed. Compound chaetae heterogomph, with short blades. Dorsal and ventral simple chaetae on some parapodia. Pharynx wide, without papillae on opening, pharyngeal tooth stout, small, located posteriorly on lateral position of pharynx. Proventricle massive, barrel-shaped, long and large. Pygidium with 2 long, filiform anal cirri. Reproductive mode unknown.

Species and distribution. Only three known species. The genus is only known in tropical areas of the West Pacific, and Indic Ocean. *Psammosyllis aliceae* Westheide, 1990; *Psammosyllis curticirris* (Hartmann-Schröder, 1983); *Psammosyllis wui* Ding & Westheide, 1997.

Bibliography. Westheide (1990); San Martín & Hutchings (2006).

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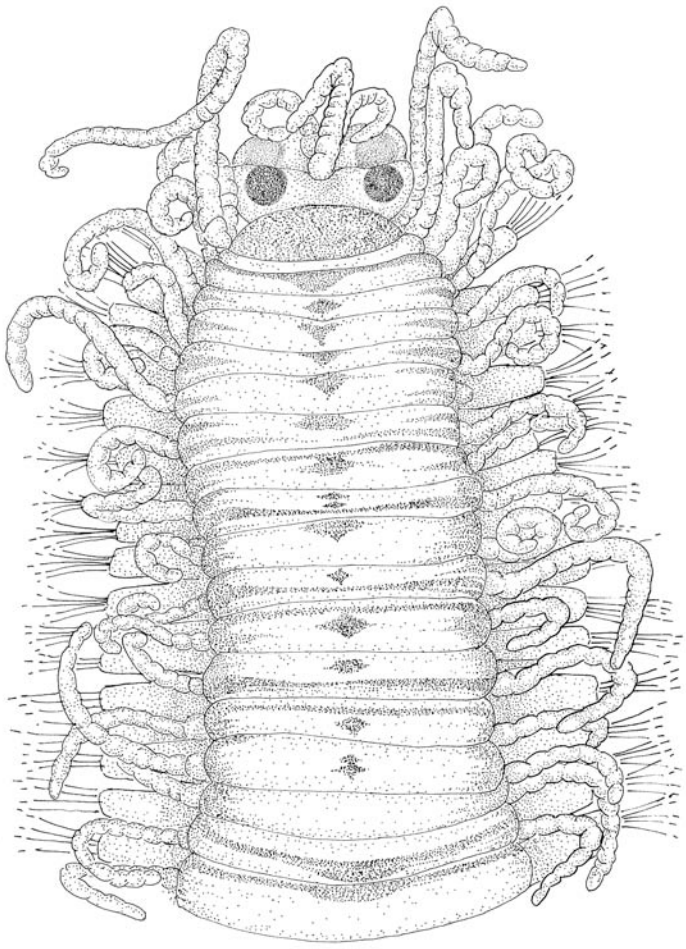
DISCUSIÓN



Los avances en taxonomía

Los avances en sistemática

DISCUSIÓN

Nuestro objetivo, al abordar un campo de estudio tan extenso como es el de la Familia Syllidae, no fue el de intentar solucionar todas las lagunas en el conocimiento de estos pequeños animales. Sabíamos desde el principio que era tarea de más de una vida de dedicación la de organizar la familia. Sin embargo, a lo largo de estos años hemos ido consiguiendo pequeños avances y alcanzando pequeñas metas. Pensamos que la contribución realizada en esta tesis doctoral es fundamentalmente la de servir de base, de cimientos para ese largo trabajo de organización sistemática de los sílidos.

Llegados a este punto, en la fase última de la realización de una tesis doctoral, nos gustaría hacer una revisión de todos esos pequeños progresos, que se han desglosado en cada uno de los cuatro bloques de la presente memoria.

Los avances en taxonomía

Las revisiones taxonómicas de géneros y especies de la familia han resultado ser de una enorme utilidad para avanzar en nuestro conocimiento sobre el grupo. Las tablas comparativas y el ejercicio de síntesis de la información acumulada sobre unos taxones son fundamentales para el avance científico en el campo de la sistemática, en esta línea encontramos varios trabajos que nos han sido de enorme utilidad (p. ej. Licher, 1999; San Martín, 2003; Nygren, 2004). En nuestro caso, el estudio de la nueva especie *Opisthosyllis leslieharrisae* nos permitió elaborar una tabla comparativa que aunó todas las especies del género *Opisthosyllis* descritas hasta el momento (ver Bloque I.4). Al mismo tiempo elaboramos una revisión de la diagnosis del género y un reconocimiento de los taxones no válidos. Ese trabajo de revisión taxonómica fue fundamental para la elaboración de posteriores estudios como el de los sílidos de Indonesia donde volvimos a encontrar dos especies más del género (*O. flaccida* y *O. mariae*) (Bloque I.5). Las especies del género *Syllis* con caracteres similares a la especie *Syllis marugani* fueron también revisadas en una tabla comparativa donde se pusieron de manifiesto sus similitudes morfológicas (Bloque I.2). Posteriormente dichas similitudes resultaron ser el reflejo de un parentesco evolutivo (ver Bloque III.1). Por otro lado, el estudio de la especie *Alcyonosyllis exiliformis* nos permitió

plantearnos la necesidad de establecer las diferencias entre el género *Alcyonosyllis* y otros géneros similares como *Syllis, Haplosyllis* y *Trypanoseta*. Elaboramos una nueva diagnosis del género incluyendo caracteres que no se habían asociado previamente con este taxón y propusimos un listado de posibles especies de *Alcyonosyllis* previamente descritas en otros géneros. También proporcionamos una nueva diagnosis del género *Trypanoseta*, pero por razones diferentes. En este caso, nos encontramos con lo que podía haber sido una incorrecta aplicación de las normas de nomenclatura animal. Redescribimos la especie *Trypanoseta ohma* y enmendamos dicho *lapsus* nominal (Bloque I.3).

A lo largo del trabajo de identificación del material estudiado, hemos podido constatar la importancia de determinados caracteres a los que tradicionalmente no se les ha concedido demasiada importancia. Tal es el caso de la coloración. Numerosas especies descritas en esta tesis doctoral presentan un llamativo patrón de pigmentación, tal es el caso *de Odontosyllis leslieharrisae*, *O. undecimdonta*, *Haplosyllis crassicirrata*, *Amblyosyllis speciosa*, *Syllis marugani*, *S. rubicunda*, etc. (Bloque I). Varios autores han llamado la atención sobre la coloración de los sílidos (Glasby y Watson, 2001; Nygren, 2004; Çinar, 2005), pero nunca se había considerado un carácter diagnóstico, principalmente porque no se puede aplicar por igual a todas las especies. La coloración de muchas especies de sílidos es desconocida, ya que los ejemplares preservados en alcohol pierden con frecuencia los pigmentos, siendo imposible conocer los colores del animal en vida. Además, muchas especies son transparentes o blanquecinas (San Martín, 2003). Sin embargo, el color tiene un importante valor biológico, ya que puede responder a adaptaciones al medio, como posibles procesos de mimetismo como ocurre en especies de *Alcyonosyllis* y *Haplosyllis* que adquieren la coloración del coral o la esponja hospedadora (Fauchald y Jumars, 1979; Glasby, 2000), o incluso de aposematismo, aunque en este último caso no disponemos de evidencias constatadas (Pleijel, 2001). Igualmente puede representar un dimorfismo sexual (estolones "*Polybostrichus*" y "*Sacconereis*" en Autolytinae) (Gidholm, 1967) y ser fundamental en la atracción entre sexos (casos documentados de fluorescencia en *Odontosyllis*) (Glasby, 2000; Pleijel, 2001). Actualmente, los avances tecnológicos, tanto en las técnicas de muestreo como preservación del material, como en los equipos de laboratorio (microscopios, lupas) están haciendo posible que se recoja más información de los animales que descubrimos de lo que se venía haciendo durante los siglos XIX y XX. Son numerosos los autores que incorporan la descripción del

patrón de coloración así como características sobre el hábitat que puedan ser posteriormente relacionadas con la morfología del animal (Musco & Giangrande, 2005; Çinar, 2003, 2005).

Los trabajos de relación entre estructuras morfológicas y hábitat de los organismos están empezando a tener una mayor trascendencia. En especies de *Haplosyllis*, *Syllis*, *Alcyonosyllis* y *Brachiosyllis* existen hipótesis acerca de la relación entre unos tipos concretos de sedas (sedas simples por procesos de fusión o sedas con forma de uñas de gato) y los organismos con los que viven asociados (Martin y Britayev, 1998; Martin *et al.*, 2002). Estas teorías han sido apoyadas por los resultados obtenidos en esta tesis (Bloque I). Quizás, las hipótesis más conocidas y más desarrolladas sobre adaptaciones morfológicas al medio son las que han sido descritas para la fauna intersticial. En poliquetos se han llevado a cabo numerosos trabajos que nos permiten conocer mejor las adaptaciones particulares a este medio (Westheide 1971, 1974, 1984, 1987, 1990). El acortamiento o incluso supresión de las fases larvarias y el desarrollo de cuidados parentales han sido ampliamente relacionados con los animales que viven en los intersticios que quedan entre los granos de arena. En esta tesis doctoral hemos podido comprobar esta relación hábitat-morfología durante el estudio de *Syllis botosaneanui* como una especie intersticial vivípara (Bloque I.1). La presencia de esta especie vivípara en aguas mexicanas ha sido comprobaba posteriormente por otros autores (Domínguez-Castañedo, en realización).

Los avances tecnológicos también nos están permitiendo conocer con más detalle la anatomía del grupo. Por ejemplo, hemos podido detectar caracteres previamente no descritos como es el caso de la existencia de bandas ciliares en el dorso de *O. undecimdonta*, y en los cirros de *A. speciosa*, las proyecciones en las sedas pseudospinígeras en *E. longicornis*, los detalles de la espinulación de *Trypanoseta ohma*, la posición y forma del diente faríngeo en *O. flaccida*, etc. (Bloque I.1, 3, 5). Detalles similares han sido incorporados para otras especies en trabajos recientes como los de San Martín *et al.* (en prensa y en espera de aceptación). Por otro lado, estos avances tecnológicos nos han permitido detectar errores en las interpretaciones de distintas estructuras de algunos taxones. Tal es el caso de los géneros *Allaudella* y *Exogonella*, que fueron descritos como nuevos géneros, entre otras características, por carecer de cirros. Sin embargo, gracias a la mayor precisión y aumento de visión de los microscopios actuales, hemos podido reconocer esas estructuras y colocar cada

especie en los géneros correspondientes ya descritos (*Odontosyllis* y *Paraexogone* respectivamente) (Bloque II).

Durante el estudio, se han encontrado especies cuya identificación no es totalmente segura, como *Syllis* cf. *mayeri*, *S.* cf. *parapari*, *S.* cf. *cornuta* y *S.* cf. *cruzi* (Bloque I.5). Estas especies han aparecido en nuestro estudio en localidades muy alejadas del área geográfica en la que fueron descubiertas (por ejemplo Belice y el Mar Mediterráneo, Atlántico e Índico, Mar del Norte e Índico, etc.). Los ejemplares que nosotros estudiamos presentan algunas características diferentes a las correspondientes series tipo de las especies a las que han sido asignados, pero estas diferencias son, en algunos casos poco claras, y en otros casos de desconocido desarrollo a lo largo de la vida del animal. Estas características como la longitud de los cirros o como la transición entre cirros "cortos" y cirros "largos", la longitud del proventrículo y/o de la faringe, la aparición de áreas glandulares en algunos segmentos, etc. parecen ser bastante lábiles en el cuerpo de los sílidos (San Martín, 2003).

Conocemos poco acerca del desarrollo postembrionario de los poliquetos en general (Glasby, 2000), por ejemplo, acerca de procesos de neotenia que puedan explicar diferentes proporciones entre estructuras presentes a lo largo de la vida del animal. La información de la que disponemos sobre el sistema hormonal y desarrollo glandular durante determinados procesos, como puedan ser los reproductivos, es muy incipiente. Aunque se ha propuesto una posible zonación en el cuerpo de los sílidos (San Martín, 2003), los cambios en las estructuras a lo largo de los diferentes segmentos del animal suelen ser muy graduales. Todas estas razones, muy relacionadas con la posesión de un cuerpo blando y sin esqueleto, hacen que las diferencias perceptibles con nuestra vista sean muy difíciles de delimitar. Estas diferencias no son estáticas ni permanentes y por tanto, su utilidad en taxonomía es insuficiente, dado el estado de nuestro conocimiento. Sin embargo, la creciente comprensión de los procesos dinámicos más que de las estructuras estáticas en invertebrados, podrá indudablemente ayudarnos a comprender el mundo de estos organismos y reorganizar así nuestras técnicas de conocimiento y nuestro esquema mental (que se traducirán en la taxonomía y sistemática).

Por otro lado, en ocasiones no hay ninguna aparente divergencia morfológica entre individuos de lugares geográficos muy alejados y sin aparente conexión. Hasta el momento, se han citado numerosos casos de aparente "cosmopolitismo" en sílidos. Tal es el caso de las *especies S. hyalina*, *S. armillaris*, *S. gracilis*, *B. exilis*, *H. spongicola*, etc. que han sido

propuestas como posibles complejos de especies en la presente tesis doctoral (Bloque I. 1, 3, 5, 6) así como en trabajos previos (Martin *et al.*, 2002; Martín y Britayev, 1998, San Martín, 2003, Musco y Giangrande, 2005, Lattig *et al.*, 2007). Las especies *S. hylina* y *S. armillaris* no están bien caracterizadas, los caracteres diagnósticos que las definen varían dentro de una misma población siendo en ocasiones muy difícil establecer los límites entre una y otra. Las diferencias entre ambas especies son a menudo sólo perceptibles en las sedas de la parte posterior de los ejemplares adultos, con lo que volvemos a estar frente a un problema de desconocimiento de los procesos postembrionarios y de sus modificaciones asociadas.

El caso de *S. gracilis*, *H. spongicola* y *B. exilis* es diferente, las tres son especies definidas por un tipo muy concreto de sedas. En *S. gracilis* y en *H. spongicola* las sedas son simples ypsiloides o simples con dos procesos terminales, respectivamente, mientras que aparecen en forma de uña de gato en *B. exilis*. Estas formas tan llamativas han hecho que sean especies de fácil identificación, de manera que en distintos estudios a lo largo del mundo se han asignado poblaciones enteras a estas especies sin revisar si existen diferencias en el resto de las estructuras propias de cada género. En este trabajo se aportan datos suficientes como para considerar que, en realidad, se trata de especies diferentes agrupadas bajo un mismo nombre. Al mismo tiempo hemos descrito especies con características llamativas similares a las que aparecen en estas especies problemáticas pero con notables diferencias en otros caracteres (ver descripciones y discusión de las especies *S. ypsiloides* y *S. komodoensis*) (Bloque I. 5). En un futuro, será necesario elaborar estudios más focalizados en cada problemática particular, que precisarán de la revisión del material recolectado por todas partes del mundo. Probablemente incluso sea necesaria la incorporación de nuevas técnicas y fuentes de información como los métodos de secuenciación de ADN y proteínas para diferenciar cada una de las especies (Westheide & Hass-Cordes, 2001).

Al mismo tiempo, nos encontramos con que nuestro objeto de estudio son seres vivos con una enorme capacidad de dispersión. Es decir, es posible que realmente estemos ante la misma especie que aparece, gracias a procesos de migración, en lugares alejados del globo. Tales procesos han sido ampliamente estudiados entre el Mar Rojo y el Mediterráneo y son conocidos como migraciones Lessepsianas (Ergen *et al.*, 2002; Ergev *et al.*, 2003; Çinar, 2006; Çinar y Ergen, 2002, 2005; Çinar *et al.*, 2005, 2006; Zenetos *et al.*, 2005). Varios sílidos son reconocidas especies migradoras, tales como *Eusyllis kupfferi*, otras fueron

consideradas migradoras, como *B. exilis*, pero actualmente se consideran complejos de especies (Çinar y Ergen, 2003; Ergen *et al.*, 2002). Nosotros hemos explicado la presencia de las especies *Exogone breviantennata* como resultados de una posible migración Lessepsiana y de *Syllis bella* como una migración entre el Caribe y el Mediterráneo (Bloque I.6). En el segundo caso se apuntó el tráfico marítimo como posible vehículo de transmisión ya que las áreas geográficas están bastante alejadas. Se han realizado trabajos similares que estudian posibles migraciones en poliquetos (Nishi y Kato, 2004) pero, de nuevo, nuestro conocimiento sigue siendo sólo incipiente. Son tantas las áreas geográficas a lo largo del planeta que permanecen sin prospectar que a veces, cualquier hipótesis migratoria carece de datos que la sustenten. Por otro lado, para evitar que se mantengan las confusiones en los procesos de identificación, son urgentemente necesarias revisiones globales de las especies conflictivas (como se ha señalado anteriormente). Además, aunque existen trabajos que se centran en la actualización de catálogos de poliquetos (Çinar y Gambi, 2005; Salazar-Vallejo y Londoño, 2004) éstos, así como revisiones globales de las distintas familias de poliquetos siguen siendo insuficientes (Musco y Giangrande, 2005). Por último, consideramos necesario relacionar los organismos que estudiamos con los procesos globales medioambientales. En esta línea, Musco y Giangrande (2005) ofrecieron una hipótesis ("la tropicalización" del Mediterráneo) que podía explicar los cambios paulatinos en la fauna de sílidos del Mediterráneo en relación con el aumento de la temperatura de los mares del que somos testigos desde hace varias décadas.

Por otro lado, la familia cuenta con algunos géneros asombrosos, por lo peculiar de sus estructuras y su escasa representación (la mayoría géneros monotípicos cuyas especies tipo estaban sólo representadas por un holotipo y en algunas ocasiones un paratipo). Algunos de estos géneros inusuales, muestran una mezcla de características que son bastante constantes en otros géneros y subfamilias y en consecuencia, se han utilizado para diferenciar grupos de la taxonomía tradicional (ver Bloque II). Por ejemplo, las proyecciones nucales externas en *Nuchalosyllis*, *Clavisyllis* y *Lamellisyllis*, son caracteres diagnósticos para Autolytinae; los palpos completamente fusionados en *Anguilosyllis*, son caracteres diagnósticos para Exogoninae; la presencia de un arco faríngeo ventral de dentículos junto con un diente en *Brachysyllis*, son características excluyentes de otros géneros, etc. Otros géneros en la familia, como *Amblyosyllis* y *Parahaplosyllis*, tienen una faringe larga y enrollada (la misma que

Autolytinae), pero su reproducción es, respectivamente por epigamia y escisiparidad posterior sin dimorfismo sexual en los estolones. El estudio de estas características en estos taxones reveló notables incoherencias en la clasificación tradicional de los sílidos.

Como fruto de todo este trabajo, hemos elaborado numerosas redescripciones, revisiones parciales de géneros y especies, hemos detectado numerosas sinonimias y nuevas combinaciones. Igualmente, los trabajos de revisión citados anteriormente han permitido la posterior elaboración de nuevos estudios no incluidos en esta tesis doctoral. Estos trabajos han sido elaborados de manera paralela o están actualmente en proceso de realización. Tal es el caso de la revisión de todo el género *Opisthosyllis* (en realización), la descripción de un nuevo género (*Tetrapalpia* n. g.) a partir de la revisión de una especie erróneamente asignada a *Opisthosyllis* (San Martín *et al.*, en prensa), la propuesta de un nuevo género (*Beatlesyllis* n. g.) a partir del estudio de la especie japonesa *Syllis nipponica* (San Martín, López y Aguado, en espera de aceptación; y San Martín, Licher y Aguado, en prep., respectivamente), la descripción de otro nuevo género en espera de aceptación (*Megasyllis* n. g. por San Martín, Hutchings y Aguado, en espera de aceptación) a partir de varias especies de *Syllis* consideradas previamente por varios autores como un grupo aparte dentro del género (*Syllis corruscans, Syllis inflata, Syllis heterosetosa* y la nueva especie que aquí describimos *Syllis multiannulata*), la revisión del género *Haplosyllides*, redescripción de *H. aberrans* y descripción de una nueva especie del género (Martín, Britayev y Aguado, en espera de aceptación), etc.

La experiencia adquirida a lo largo del estudio de la anatomía de los sílidos nos puso en disposición de abordar un análisis filogenético con el que pudiéramos inferir las relaciones evolutivas dentro de la familia.

Los avances en sistemática

Son pocos los estudios centrados en la filogenia del grupo hasta la presente tesis doctoral. Además los únicos trabajos previos (Licher, 1999; Nygren, 1999; Nygren & Sundberg, 2003 y Nygren, 2004) estaban centrados en problemas concretos y solo pretendían abordar el análisis de las relaciones evolutivas de algunos géneros (*Syllis*) o subfamilias (Autolytinae). Indudablemente, estos trabajos fueron decisivos en la elaboración de nuestras hipótesis, más

globales, que han pretendido arrojar algo de luz a la filogenia de la familia Syllidae en su conjunto.

Hemos abordado el estudio de las relaciones filogenéticas a partir de dos fuentes de datos diferentes: datos moleculares, en concreto secuencias de ADN, y datos morfológicos, incluyendo también los modos reproductivos (Bloque III.1, 2). Además, ambos análisis partieron de un conjunto diferente de taxones, en el análisis molecular (Bloque III.1) se incluyeron 88 especies de sílidos pero sólo 29 géneros. Sin embargo, el análisis morfológico (Bloque III.2) reunió todos los géneros descritos y aceptados hasta el momento, una vez llevada a cabo la revisión de géneros dudosos en la familia (Bloque II). Aún así, los resultados, en términos generales, se apoyaron entre sí y también concordaron con los resultados parciales que habían obtenido previamente otros autores (Licher, 1999; Nygren, 1999; Nygren & Sundberg, 2003 y Nygren, 2004).

La secuenciación de ADN (genes 18S, 16S y COI) resultó bastante complicada, principalmente en el caso del gen mitocondrial COI. Cambiamos numerosas veces los protocolos, modificamos distintas variables e incluso trabajamos con distintos "*primers*" hasta que pudimos reunir una cantidad de datos suficiente como para apoyar una hipótesis evolutiva robusta. Dichas dificultades en la secuenciación de este gen parecen ser comunes en otras familias de poliquetos (Halanych y Janosik, 2005). Una de las posibles soluciones podría consistir en la localización de "*primers*" específicos para anélidos, e incluso más concretamente para sílidos. Son muchos los aspectos que aún quedan por investigar en relación con el genoma de los poliquetos, en especial teniendo en cuenta que únicamente se conoce el genoma mitocondrial completo de cuatro anélidos (Boore y Brown, 2000; Boore, 2001; Halanych y Janosik, 2005). Por otro lado, la secuenciación del gen 18S también puede conducir a resultados totalmente inesperados. Por ejemplo, intentando obtener el gen 18S de *Syllis nipponica*, obtuvimos dicho gen pero de un parásito interno de esta especie perteneciente al grupo de los Haplosporideos (Siddall y Aguado, 2006). Esos parásitos se habían descrito por primera vez asociados a los poliquetos (Caullery y Mesnil, 1889), pasando después a conocerse principalmente como parásito de moluscos. La secuenciación del ADN de este parásito permitió comprobar que estos protozoos viven dentro de poliquetos. Al mismo tiempo, contribuyó a la realización de un análisis filogenético del grupo de los Haplosporideos. La investigación a un nivel molecular de los anélidos poliquetos se encuentra

todavía en un estado incipiente y son numerosas las preguntas que quedan aún por resolver (McHugh, 2005).

Los trabajos de filogenia molecular y morfológica presentados en esta tesis apoyan la hipótesis de que hay tres grupos naturales dentro de sílidos (Autolytinae, Exogoninae y Syllinae) y un cuarto grupo que es artificial (Eusyllinae). Curiosamente, si tenemos en cuenta la historia de la taxonomía de sílidos (ver introducción), estos tres grupos naturales fueron descritos y considerados como subfamilias en primer lugar (a finales del s. XIX); y no fue hasta 14 años después que se incluyó un cuarto grupo adicional (Eusyllinae) que reunió al resto de los géneros. Los estudios filogenéticos nos dicen que la clasificación elaborada inicialmente era la correcta y que la inclusión de un cuarto grupo respondió principalmente a una necesidad práctica.

Las relaciones evolutivas entre los distintos tipos de reproducción han sido objeto de numerosos estudios, entre los que destacan los trabajos de Malaquin (1893), Potts (1911), y Garwood (1991). Dependiendo de los trabajos, los procesos de epigamia y esquizogamia han sido considerados indistintamente como primitivos y derivados en la familia Syllidae. Estas primeras hipótesis se apoyaron únicamente en el conocimiento descriptivo que se tenía de ambos procesos. No ha sido hasta principios del siglo XXI, cuando se han introducido las técnicas de inferencia filogenética para elaborar hipótesis evolutivas sobre la reproducción en sílidos.

A la luz de los resultados que hemos ido obteniendo, la epigamia podría ser considerada como el estado reproductivo original en la familia mientras que la esquizogamia consistiría en una adquisición secundaria. A su vez, la esquizogamia en Autolytinae y Syllinae, podría tener orígenes diferentes, siendo un claro ejemplo de homoplasia ya que existen numerosas diferencias en ambos grupos, principalmente en el tipo de estolones. Los procesos de incubación en Exogoninae podrían también tener su implicación evolutiva ya que, aunque no está confirmado por todos los estudios, parece que hay dos líneas evolutivas diferentes que se distinguen fundamentalmente por desarrollar incubación dorsal y ventral, respectivamente. Sin embargo, aunque los procesos reproductivos parecen ser bien distinguibles dentro de los sílidos, también hay casos de homoplasia principalmente en las estrategias de incubación (en *Nudisyllis*, *Pionosyllis* y *Syllides*, y en *Amblyosyllis* y *Anoplosyllis*) que podrían ser

explicados como adaptaciones a determinados medios concretos. Sin embargo, estas hipótesis necesitan más datos sobre los que apoyarse.

El estudio filogenético de la familia también nos ha permitido comprobar que determinados géneros son parafiléticos, como es el caso de *Syllis* y *Pionosyllis* y que, por tanto, necesitan una reorganización (en el caso de *Pionosyllis* en San Martín, López y Aguado, en espera de aceptación). Pudimos comprobar igualmente que las especies de *Syllis* propuestas como próximas a la especie *Syllis marugani* están probablemente emparentadas (Bloque III.1) y que las especies *S. gracilis*, *S. armillaris* y *S. hyalina*, cuyos problemas taxonómicos se han mencionado previamente, están muy cercanas desde un punto de vista evolutivo. Igualmente, comprobamos que el viviparismo aparece independientemente en distintos grupos monofiléticos de tal manera que las hipótesis que plantean esta estrategia como una adaptación al medio (Westheide 1971, 1974, 1984, 1987, 1990) aparecen reforzadas por nuestros resultados.

Por último, otro resultado de gran relevancia es la identificación de un grupo monofilético bien definido que parece estar diferenciado del resto de los sílidos (Clado I en los análisis moleculares y morfológicos) que es designado como la nueva subfamilia Anoplosyllinae (ver Bloque IV).

Sin embargo, la monofilia de la familia no ha podido ser demostrada, en el caso de los análisis moleculares porque los valores de soporte son bajos, en el caso de los análisis morfológicos porque las relaciones con la familia Sphaerodoridae son aún inciertas. Ambos casos sugieren que el posible estatus de grupo natural (monofilético) de la Familia Syllidae precisa aún de un estudio más detenido. Igualmente, hay varios géneros cuyas relaciones con el resto de sílidos permanecen ambiguas. Estos géneros son muy diferentes al resto, pero se distinguen por poseer características únicas (Autapomorfías), que carecen de sentido evolutivo en un estudio a nivel genérico (por ejemplo, *Murrindisyllis*, *Miscellania*, *Neopetitia*, *Nooralia*, *Anguilosyllis*, *Clavisyllis* y *Lamellisyllis*) (ver Bloque II).

Esta falta de resolución, podrían encontrar varias explicaciones. La primera de ellas podría consistir en la tendencia de los seres humanos de encontrar las mismas estructuras en los diferentes organismos. La mayoría de las estructuras morfológicas en sílidos se distinguen por su posición en el cuerpo y por su forma. Por ejemplo, los órganos nucales se definen por su función, pero en realidad, se identifican por su posición después del prostomio. Lo mismo

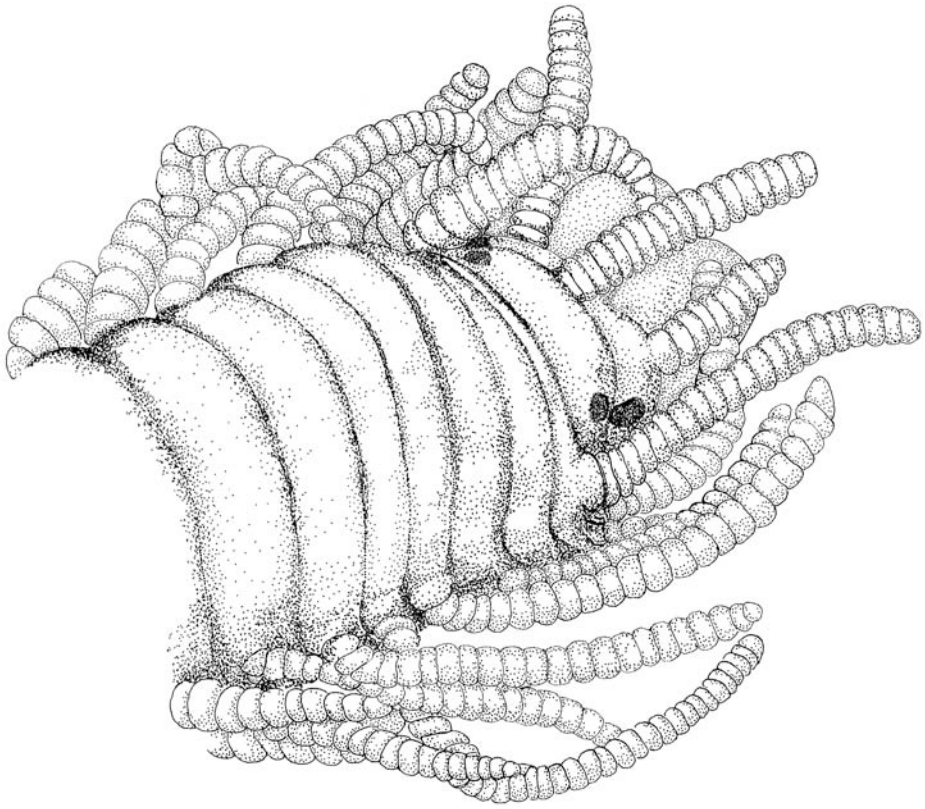
sucede con el proventrículo. La similitud entre las estructuras externas no significa necesariamente que sean lo mismo pero mientras no existan estudios que evidencien su organización interna, no podemos decir que son diferentes. Esta tendencia afecta a los métodos de inferencia filogenética ya que diferentes estructuras pueden ser codificadas como la misma característica resultando en un alto grado de homoplasia, con la consiguiente falta de resolución en los resultados. Una segunda posibilidad podría explicar la variabilidad anatómica de estos animales como consecuencia de una alta plasticidad estructural. El cuerpo de los sílidos está limitado por un patrón regular y constante de repetición seriada de estructuras (segmentación). Pero los cambios en la forma, tamaño e incluso de la función de estas estructuras podrían ser bastante flexibles, incluso durante la vida del animal. Esta hipótesis podría explicar también las diferencias entre las poblaciones. Por ejemplo, la especie *Amblyosyllis speciosa* se ha citado como una especie epigámica, mostrando las típicas modificaciones de este modo de reproducción (Bloque I. 3), pero también se han encontrado otros ejemplares que no muestran modificación alguna incubando sus huevos en masas gelatinosas (Pernet, 1998). Esta plasticidad estructural podría explicar, del mismo modo las diferencias durante la ontogenia (véase la discusión acerca de las estructuras faríngeas en *Haplosyllides* y *Trypanosyllis* en el Bloque III.2). Otra explicación podría consistir en entender la falta de resolución en las relaciones evolutivas de estos géneros como la consecuencia de nuestra ignorancia. Esta opción mantiene la esperanza de resolver el problema en un futuro cercano a medida que nuestros conocimientos vayan aumentando progresivamente.

A pesar de todas estas dudas y distintas aproximaciones a la difícil y laberíntica sistemática de los sílidos, y a pesar también de nuestros todavía escasos conocimientos, los datos morfológicos y moleculares disponibles junto con la metodología cladística han sido capaces de exponer la primera historia evolutiva de todos los géneros de sílidos, que indudablemente será contrastada, criticada y modificada por posteriores y, probablemente, numerosos estudios.

A partir de todos los resultados obtenidos en esta tesis y los trabajos que se han ido realizando de manera paralela (principalmente San Martín, Hutchings y Aguado, en prensa, y en espera de aceptación; San Martín, López y Aguado, en espera de aceptación) y numerosos

trabajos previos (Licher, 1999; Nygren, 2004; San Martín, 2003, 2005; San Martín y Hutchings, 2006) pudimos proponer una nueva clasificación para la familia Syllidae (Bloque IV). Esta clasificación pretende reflejar el conocimiento actual sobre el grupo y pretende, igualmente, ajustarse a nuestros conocimientos acerca de la historia evolutiva de los sílidos. De esta manera, las tres subfamilias (Syllinae, Autolytinae y Exogoninae) se mantienen al haber sido propuestas como grupos naturales. Añadimos una cuarta subfamilia (Anoplosyllinae) basándonos en los resultados de los análisis filogenéticos y mantenemos, aunque sin categoría taxonómica, el grupo "eusyllinae" a la espera de obtener evidencias de la posible monofilia (Bloque II.1). Desafortunadamente, varios géneros, para los que no tenemos información acerca de sus relaciones evolutivas, permanecen de manera transitoria dentro de los "*incertae sedis*".

CONCLUSIONES



1. Conclusiones taxonómicas
2. Conclusiones de la revisión de géneros enigmáticos
3. Conclusiones en cuanto a las relaciones filogenéticas
4. Conclusiones sistemáticas

CONCLUSIONES

1. Conclusiones taxonómicas

- En total, se han identificado 97 especies pertenecientes a 31 géneros.
- Se han descrito 10 especies nuevas del estado de California (EEUU), Japón e Indonesia: *Opisthosyllis leslieharrisae*, *Haplosyllis crassicirrata*, *Syllis marugani*, *Syllis multiannulata*, *Syllis pilosa*, *Syllis rubicunda*, *Opisthosyllis mariae*, *Syllis komodoensis*, *Syllis villenai* y *Syllis ypsiloides.*
- Se han realizado revisiones de los géneros *Opisthosyllis*, *Alcyonosyllis* y *Trypanoseta*, estableciendo nuevas diagnosis, reuniendo todas las especies correspondientes a cada género y tablas comparativas en casos particulares.
- Se ha propuesto el nombre genérico *Trypanoseta* para sustituir el de *Geminosyllis* en aplicación del Principio de Prioridad del Código Internacional de nomenclatura Zoológica.
- Se han presentado 11 nuevas combinaciones: *Trypanoseta ohma*, *Syllis nipponica*, *Alcyonosyllis exiliformis*, *Opisthosyllis flaccida*, *Syllis monilata*, *Syllis pigmentada*, *Syllis setoensis*, *Syllis glarearia*, *Salvatoria heterocirrata*, *Salvatoria mediodentata* y *Paraehlersia articulata*.
- Se ha traspasado la especie *Pionosyllis articulata* al género *Paraehlersia*. La especie *Eusyllis habei* se ha sinonimizado con *E. assimilis*, *Odontosyllis fulgurans japonica* se ha sinonimizado con *O. japonica*, las citas de la especie *O. brunnea* de Japón se han considerado como correspondientes a la especie *Syllis pectinans*. *Syllis augeneri* previamente sinonimizada con *S. gracilis* se ha redescrito y se ha propuesto como válida.
- Se han expuesto 25 nuevas citas de especies para distintas áreas geográficas: *Exogone arenosa* y *Streptosyllis websteri* para el Pacífico; *E. dispar*, *E. longicornis*, *Salvatoria mediodentata*, *Pionosyllis heterocirrata* y *Syllis glarearia* para Panamá; *Inermosyllis balearica* para el Mediterráneo oriental; *Eusyllis assimilis*, *Nudisyllis tinihekea*, *Paraehlersia ehlersiaeformis* y *Branchiosyllis exilis* para Japón; *E. assimilis*, *E. lamelligera*, *Odontosyllis freycinetensis*, *Sphaerosyllis georgeharrisoni*, *B. exilis*, *B. maculata*, *B. verruculosa*,

Oisthosyllis flaccida, S. aciculata, S. augeneri, S. lutea, S. setoensis y *Trypanosyllis zebra* para Indonesia.

- Se han identificado los siguientes complejos de especies: *Syllis armillaris, S. hyalina, S. gracilis*, *Branchiosyllis exilis* y *Exogone naidina.*
- Se han descrito nuevas características no citadas previamente para las especies: *Exogone longicornis* (con proyecciones laterales en los mangos de las sedas pseudospiníferas), *Amblyosyllis speciosa* (con bandas rugosas sobre el cuerpo y cilios en los cirros) y *Odontosyllis undecimdonta* (con bandas ciliares sobre la superficie del cuerpo y reproducción por epigamia).
- Se ha descrito la especie *Syllis botosaneanui* como vivípara.
- Se ha confirmado la presencia de *Eusyllis kupfferi* (posible emigrante Lessepsiano) en aguas libanesas. Se han identificado las especies *Exogone breviantennata* y *Syllis bella* como posibles especies migradoras y se han expuesto posibles hipótesis acerca de su origen en el Mediterráneo oriental.
- Se han reconocido cinco especies de identificación dudosa por presentar distribuciones disyuntas y caracteres morfológicos variables: *Syllis* cf. *mayeri, S.* cf. *cornuta, S.* cf. *parapari* y *S.* cf. *cruzi*.
- Se ha demostrado una gran similitud entre la fauna de sílidos de Indonesia, Japón y Australia.
- Se ha apoyado la hipótesis de que la aparición de sedas simples en algunas especies de los géneros *Syllis*, *Haplosyllis*, *Alcyonosyllis*, y probablemente *Trypanoseta* y *Parahaplosyllis* parecen proceder de la fusión entre mango y artejo de una seda originariamente compuesta. Se ha podido relacionar la aparición de este tipo de sedas con la asociación a otros organismos (esponjas o corales).

2. Conclusiones de la revisión de géneros enigmáticos

- Se han redescrito los géneros *Anguillosyllis*, *Brachysyllis*, *Clavisyllis, Lamellisyllis* y *Nuchalosyllis.*
- *Brachysyllis* se ha considerado un género válido y se diferencia de *Dioplosyllis* con el que se había sinonimizado.

- Se han justificado como no válidos los géneros: *Braniella* por ser sinónimo de *Anguillosyllis*; *Alluaudella* por ser sinónimo de *Odontosyllis* y *Exogonella* por ser sinónimo de *Paraexogone*.
- *Exogonoides* se ha considerado como *nomina dubia* porque sus relaciones con el resto de los sílidos no pudieron ser establecidas, incluso, tenemos dudas razonables de que pueda ser considerado un sílido.

3. Conclusiones en cuanto a las relaciones filogenéticas

- Se han propuesto las subfamilias Syllinae, Autolytinae y Exogoninae como grupos monofiléticos. Eusyllinae, sin embargo, ha resultado ser un grupo claramente parafilético.
- Los géneros *Astreptosyllis*, *Streptospinigera*, *Syllides*, *Streptosyllis* y *Anoplosyllis* constituyen un grupo bien diferenciado del resto de los sílidos.
- La epigamia ha resultado ser el modo reproductivo primitivo en la familia Syllidae, la esquizogamia se ha propuesto como el modo derivado que pudo haber aparecido dos veces, en Autolytinae y en Syllinae, como procesos independientes.
- Se han propuesto dos posibles líneas evolutivas dentro de Exogoninae atendiendo principalmente a los procesos de incubación dorsal y ventral.
- La incubación en las especies de *Nudisyllis*, *Syllides*, *Nooralia* y en *Pionosyllis augeneri* aparecen como procesos de paralelismos con la incubación en Exogoninae. La incubación en masas gelatinosas que presentan *Anoplosyllis* y *Amblyosyllis* es también un paralelismo.
- Se ha confirmado la aparición del viviparismo en determinadas especies de la familia como procesos de convergencia, que responden a adaptaciones al medio.
- Se han reconocido los géneros *Pionosyllis* y *Syllis* como claramente parafiléticos.
- Se han identificado las especies *Syllis gracilis, S. armillaris* y *S. hyalina* como especies con un grado de parentesco muy cercano. Los géneros *Amblyosyllis*, *Brachysyllis* y *Dioplosyllis* se han reconocido como muy próximos desde un punto de vista evolutivo.
- Se ha discutido la existencia del proventrículo en Sphaerodoridae. Se ha puesto de manifiesto la necesidad de realizar estudios anatómicos comparativos entre el proventrículo de Syllidae y Sphaerodoridae.

- Se ha demostrado la existencia de una elevada homoplasia en la familia en cuanto a caracteres morfológicos tradicionalmente usados en taxonomía como son la forma de los órganos nucales, la presencia de trépano y la articulación de los cirros.

4. Conclusiones sistemáticas

- Se ha propuesto una nueva subfamilia, la subfamilia Anoplosyllinae, que incluye a los géneros *Astreptosyllis*, *Streptospinigera*, *Syllides*, *Streptosyllis* y *Anoplosyllis*.
- Se ha propuesto una nueva clasificación de la familia Syllidae y por primera vez se han recogido todos los géneros válidos, con nuevas y actualizadas diagnosis, así como un inventario de todas las especies pertenecientes a cada uno de los géneros.

CONCLUSIONS

1. Taxonomic conclusions

- A total of 97 species and 31 genera have been identified.
- 10 new species from the California State (USA), Japan and Indonesia have been described: *Opisthosyllis leslieharrisae*, *Haplosyllis crassicirrata*, *Syllis marugani*, *Syllis multiannulata*, *Syllis pilosa*, *Syllis rubicunda*, *Opisthosyllis mariae*, *Syllis komodoensis*, *Syllis villenai* y *Syllis ypsiloides.*
- The genera *Opisthosyllis*, *Alcyonosyllis* and *Trypanoseta* have been revised and new diagnoses and lists of valid species have been provided.
- The generic name *Trypanoseta* has been proposed to substitute *Geminosyllis* in application of the Priority Principle of the International Code of Zoological Nomenclature.
- Eleven new combinations have been proposed: *Trypanoseta ohma*, *Syllis nipponica*, *Alcyonosyllis exiliformis*, *Opisthosyllis flaccida*, *Syllis monilata*, *Syllis* pigmentata, *Syllis setoensis*, *Syllis glarearia*, *Salvatoria heterocirrata*, *Salvatoria mediodentata* and *Paraehlersia articulata*.
- The species *Pionosyllis articulata* has been considered as belonging to *Paraehlersia*. The species *Eusyllis habei* is considered synonymous with *E. assimilis*; *Odontosyllis fulgurans japonica* is considered synonymous with *O. japonica*; the previous reports of the species *O. brunnea* from Japan have been considered to correspond to *Syllis pectinans*. *Syllis augeneri* previously considered synonymous with *S. gracilis* has been re-described and proposed herein as a valid species.
- 25 species have been firstly reported from different geographical areas: *Exogone arenosa* and *Streptosyllis websteri* from the Pacific Ocean; *E. dispar*, *E. longicornis*, *Salvatoria mediodentata*, *Pionosyllis heterocirrata* and *Syllis glarearia* from Panama; *Inermosyllis balearica* from the East Mediterranean; *Eusyllis assimilis*, *Nudisyllis tinihekea*, *Paraehlersia ehlersiaeformis* and *Branchiosyllis exilis* from Japan; *E. assimilis*, *E. lamelligera*, *Odontosyllis freycinetensis*, *Sphaerosyllis georgeharrisoni*, *B. exilis*, *B. maculata*, *B.*

verruculosa, *Opisthosyllis flaccida*, *S. aciculata*, *S. augeneri*, *S. lutea*, *S. setoensis* and *Trypanosyllis zebra* from Indonesia.

- Several complexes of species have been identified: *Syllis armillaris*, *S. hyalina*, *S. gracilis*, *Branchiosyllis exilis* and *Exogone naidina*.
- Several new characteristics not previously described for some species have been provided: *Exogone longicornis* (with lateral projections in the pseudospinigers fangs), *Amblyosyllis speciosa* (with organized bands of wrinkles on the surface of the body and papillae on cirri) and *Odontosyllis undecimdonta* (with ciliary bands over the surface of the body and epigamic reproduction).
- The species *Syllis botosaneanui* has been described as viviparous.
- The presence of *Eusyllis kupfferi* (possible Lessepsian migrant) in Lebanese waters has been confirmed. The species *Exogone breviantenata* and *Syllis bella* have been identified as possible migrant species. Different hypothesis to explain their origins in the eastern Mediterranean have been proposed.
- Five species have been identified as cf. because their reported localities are very disjunct and they have variable morphological characters: *Syllis* cf. *mayeri*, *S.* cf. *cornuta*, *S.* cf. *parapari* and *S.* cf. *cruzi*. Their possible differences with the closest species have been also discussed.
- A high similarity between the syllid faunas of Australia, Japan and Indonesia has been noted.
- The hypothesis about the origin of the simple chaetae in some species of several genera (*Syllis*, *Haplosyllis*, *Alcyonosyllis*, y probablemente *Trypanoseta* and *Parahaplosyllis*) as the result of a fusion process between the fang and the blade has been supported. The appearance of these simple chaetae has been proposed as related to the habitat in which these species live (generally other organism as sponges or corals).

2. Conclusions to the revision of enigmatic genera

- The genera *Anguillosyllis*, *Brachysyllis*, *Clavisyllis*, *Lamellisyllis* and *Nuchalosyllis* have been re-described.

- *Brachysyllis* has been considered as a valid genus different to *Dioplosyllis*.
- The following genera have been proposed as non valid: *Braniella* because it is considered synonymous with *Anguillosyllis*; *Alluaudella* because it is considered synonymous with *Odontosyllis* y *Exogonella* because it is considered synonymous with *Paraexogone*.
- *Exogonoides* has been proposed as *nomina dubia* because its relationships with the rest of syllids could not be established and it was not possible to find any clear syllid´s characteristic.

3. Phylogenetic conclusions

- The subfamilies Syllinae, Autolytinae and Exogoninae have been found to be monophyletic groups. However Eusyllinae has been found to be a clear paraphyletic group.
- The genera *Astreptosyllis*, *Streptospinigera*, *Syllides*, *Streptosyllis* and *Anoplosyllis* constitute a well defined group different to the rest of syllids.
- Epigamy has been proposed as the primitive condition in the Family Syllidae, while schyzogamy has been proposed as the derived condition that might have appeared twice in the family, once in Autolytinae and another in Syllinae, as independent process.
- Two possible evolutionary lines attending to the dorsal and ventral brooding modes have been proposed within Exogoninae.
- Brooding in the species *Nudisyllis*, *Syllides*, *Nooralia* and in *Pionosyllis augeneri* are proposed as parallelism with brooding in Exogoninae. The brooding in gelatinous masses found in *Anoplosyllis* and *Amblyosyllis* is also considered a parallelism.
- Viviparity has been proposed as a convergent adaptation to the interstitial life.
- The genera *Pionosyllis* and *Syllis* have been recognized as paraphyletic.
- The species *S. gracilis, S. armillaris* and *S. hyalina* have been found to be evolutionary related. The genera *Amblyosyllis*, *Brachysyllis* and *Dioplosyllis* have been found very closely related from an evolutionary point of view.
- The presence of a proventricle in the Family Sphaerodoridae has been discussed. More anatomical and comparative studies about this structure in syllids and spherodorids have been proposed as necessary.

- High degree of homoplasy has been found for several features that are traditionally applied to delineate subgroups of Syllidae, including articulation of appendages, fusion of palps, and the presence of nuchal epaulettes.

4. Systematic conclusions

- A new subfamily, the subfamily Anoplosyllinae, has been proposed. This subfamily includes the genera *Astreptosyllis*, *Streptospinigera*, *Syllides*, *Streptosyllis* and *Anoplosyllis*.
- A new classification for the family Syllidae is proposed. This classification synthesized all the recent improvements about systematics on syllids and is adjusted to our current knowledge about natural groups from an evolutionary point of view. This classification has included the current diagnoses of all recognized genera, together with a catalogue of all valid species and identification keys to genera.

TRABAJOS FUTUROS

Son numerosos los trabajos que nos quedan pendientes para terminar la revisión global de la familia. Sin embargo, consideramos que algunos de ellos son indispensables a la luz de los resultados obtenidos en esta tesis doctoral. A continuación señalamos dichos trabajos en orden cronológico de realización:

- Estudio histológico comparativo del proventrículo en las Familias Syllidae y Sphaerodoridae.
- Secuenciación del ADN (genes 18S, 16S y COI) de un mayor número de especies y géneros que los incluidos en previos análisis.
- Elaboración de una matriz con datos morfológicos (caracteres elaborados para el bloque III.1) correspondientes a las especies para las que se dispone de datos moleculares.
- Realizar un análisis combinado incorporando la mayor cantidad de información posible sobre la Familia Syllidae (datos morfológicos y moleculares).
- Comparar los resultados obtenidos mediante diferentes metodologías de inferencia filogenética: parsimonia, máxima verosimilitud y el análisis bayesiano.
- Revisar la clasificación de la familia Syllidae propuesta en esta tesis, incorporando los nuevos resultados obtenidos de la realización de los objetivos expuestos en los puntos anteriores.

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ANEXOS

Matriz morfológica de datos correspondiente al Bloque III.1

Taxa/Characters										1										2										3	
Pisione longispinulata	0	2	2	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	-	-	-	-	-	2	0	0	0	0	0	0
Nereis virens	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	-	-	1	0	0	0	0	0	0	0	1
Chrysopetalum maculata	1	2	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	2	1	2	1	0	0	0	0	0	0	0	1
Sphaerodoropsis anae	0	2	2	0	0	0	0	0	1	1	0	0	-	0	0	0	0	0	1	0	0	2	2	0	0	0	0	0	0	0	0
Alcyonosyllis phili	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	1	0	0	1	0	0	1	0	1
Amblyosyllis speciosa	1	3	0	0	1	1	1	0	0	0	0	1	0	0	0	0	0	0	1	0	1	3	3	2	0	1	0	1	1	0	1
Anguillosyllis capensis	0	3	2	0	0	0	0	0	0	0	0	0	-	0	0	0	0	0	1	0	0	2	2	0	2	1	0	0	2	0	1
Anoplosyllis edentulus	0	2	2	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0	1	0	1	1	1	0	0	1	0	0	1	0	1
Astreptosyllis acrassiseta	0	2	2	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	?	1	0	0	1	0	0	1	0	1
Bollandia antipathicola	0	1	2	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	-	-	-	-	-	1	-	?	-	-	0	?
Brachysyllis infuscata	0	3	1	0	1	1	1	0	0	0	1	1	0	0	0	0	0	0	1	0	0	3	3	0	2	1	0	0	0	0	1
Branchiosyllis oculata	1	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	1	1	0	1	0	0	1	0	1
Brania pusilla	0	2	2	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	2	0	1	1	0	0	1	0	0	1	0	1
Cicese sphaerosylliphormis	0	2	2	0	0	0	0	0	1	0	0	1	0	1	1	0	0	1	1	2	0	1	1	0	0	1	0	0	2	0	1
Clavisyllis alternata	0	1	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	5	0	0	0	?	0	1	0	1	1	0	1
Dentatisyllis mortoni	0	2	2	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	1	1	0	1	0	0	1	0	1
Dioplosyllis cirrosa	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	0	0	3	3	0	2	1	0	0	1	0	1
Epigamia labordai	?	1	1	0	0	0	0	0	0	0	?	1	0	0	0	0	0	0	1	0	1	0	0	0	1	1	0	1	2	0	1
Erinaceusyllis serratosetosa	0	2	2	0	0	0	0	0	1	0	0	1	0	1	1	0	0	1	1	2	0	1	1	0	0	1	0	0	2	0	1
Eurysyllis tuberculata	0	1	2	1	0	0	0	0	0	1	0	1	0	1	0	0	0	0	1	4	1	1	1	1	3	1	1	0	1	0	1
Eusyllis blomstrandi	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	0	1	0	1	2	0	1	0	0	0	0	1
Exogone naidina	0	2	2	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1	1	1	2	2	0	0	1	0	0	2	0	1
Geminosyllis ohma	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	1	1	0	1	0	0	1	0	1
Haplosyllides floridana	0	2	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	1	0	1
Haplosyllis spongicola	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	1	1	0	1	0	0	1	0	1
Imajimaea zonata	1	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	0	1	1	0	1	2	0	1
Inermosyllis balearica	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	1	1	1	0	1	0	0	1	0	1
Karroonsyllis exogoneformis	0	1	1	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	1	1	2	1	0	0	2	0	1
Lamellisyllis comans	0	1	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	5	0	0	0	?	0	1	0	0	1	0	1
Levidorum hartmanae	?	2	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	-	-	-	-	-	1	1	0	-	-	0	1
Miscellania dentata	0	3	2	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	2	1	1	1	0	0	1	0	0	0	0	1
Murrindisyllis kooromundrola	0	1	1	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	1	0	0	3	1	0	0	1	0	0	2	1	1
Myrianida prolifera	0	1	1	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0	1	0	0	0	0	0	1	1	0	1	2	0	1
Neopetitia amphophthalma	0	2	2	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	1
Nooralia bulgannabouyanga	0	2	2	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	1	0	1
Nuchalosyllis lamellicornis	1	0	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	1	0	1	0	1	0	0	1
Nudisyllis pulligera	0	2	2	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	1
Odontosyllis fulgurans	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0	0	1	0	1	1	1	0	0	1	0	0	1	0	1
Opisthodonta morena	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	1
Opisthosyllis brunnea	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	1	0	0	0	0	1	0	1	0	0	1	0	1
hydrozoicola	?	2	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0	1	2	0	1
Palposyllis prosostoma	0	0	0	0	0	0	0	0	1	0	0	0	-	0	0	0	0	0	1	0	0	0	1	0	2	1	0	0	1	1	1
Paraehlersia ferrugina	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	0	0	0	1	2	0	1	0	0	1	0	1
Paraexogone hebes	0	2	1	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	1	1	0	2	2	0	0	1	0	0	2	0	1
Parahaplosyllis brevicirra	0	1	1	1	0	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	1	1	1	1	3	1	0	0	0	0	1
Paraopisthosyllis ornaticirra	1	1	1	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	1	0	0	1	1	0	0	1	0	1	1	0	1
Parapionosyllis minuta	0	2	2	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	1	2	0	1	1	0	0	1	0	0	1	0	1
Paraproceraea tamana	0	2	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0	1	2	0	1
Paraprocerastea crocantinae	?	2	2	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	0	1	1	0	1	2	0	1
Parasphaerosyllis indica	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	1	0	1	0	0	1	0	1
Pionosyllis enigmatica	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	1	0	1
Plakosyllis brevipes	0	2	2	1	0	0	0	0	0	0	0	1	0	1	0	0	0	0	1	4	1	1	1	1	3	1	1	0	0	0	1
Planicirrata proceraeae	?	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	?	?	?	?	0	1	1	0	1	2	0	1
Proceraea picta	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	0	0	0	1	1	0	1	2	0	1
Procerastea halleziana	0	2	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0	1	2	0	1
Proshaerosyllis xarifae	0	2	2	0	0	0	0	0	1	0	0	1	0	1	1	0	0	0	1	2	0	1	1	0	0	1	0	0	2	0	1
Psammosyllis wui	0	2	2	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	1	1	0	0	1	0	0	2	0	1
Rhopalosyllis hamulifera	0	1	1	1	0	0	0	0	1	0	0	1	0	0	0	0	0	0	1	0	0	1	1	1	0	1	0	1	1	0	1
Salvatoria clavata	0	2	2	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	1	2	0	1	1	0	0	1	0	0	2	0	1
Sphaerosyllis hystrix	0	2	2	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0	1	2	0	1	1	0	0	1	0	0	2	0	1
Streptodontha pterochaeta	0	1	1	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	1	0	0	1	0	0	1	0	1
heterosetosa	0	2	2	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	1	0	0	1	0	0	1	0	1
Streptosyllis websteri	0	2	2	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	1	0	0	0	1	0	0	1	0	0	1	0	1
Syllides japonicus	0	1	2	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0	1	0	0	0	1	0	0	1	0	0	1	0	1
Syllis prolifera	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	1	1	0	1	0	0	1	0	1
Trypanosyllis aeolis	1	0	0	1	0	0	0	0	1	0	0	1	0	0	0	0	0	0	1	0	1	0	0	1	0	1	0	0	0	0	1
Virchowia clavata	0	2	2	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	1	0	0	0	1	1	0	1	2	0	1
Xenosyllis scabra	0	1	1	1	0	0	0	1	1	0	0	1	0	0	0	0	0	0	1	0	1	1	1	1	3	1	1	0	0	0	1

Taxa/Characters									4										5										6			
Pisione longispinulata	0	1	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	2	2	0	0	0	0	0	0	0
Nereis virens	0	2	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0
Chrysopetalum maculata	0	1	0	1	0	1	1	0	0	0	0	0	0	0	2	0	0	0	0	0	0	1	1	1	0	0	1	?	?	?	0
Sphaerodoropsis anae	0	0	0	1	1	0	1	0	0	0	0	0	0	1	-	0	0	-	-	-	0	-	-	-	-	-	-	1	5	0	0
Alcyonosyllis phili	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0
Amblyosyllis speciosa	1	1	2	3	1	0	1	0	0	0	0	0	0	0	0	0	1	2	2	2	0	3	3	3	0	0	1	0	0	2	0
Anguillosyllis capensis	0	0	0	2	1	0	0	0	0	0	2	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Anoplosyllis edentulus	0	1	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1	0	0	0	0
Astreptosyllis acrassiseta	0	1	0	1	1	0	0	0	0	0	1	0	1	0	0	0	0	0	1	1	1	1	0	0	1	0	1	?	?	?	0
Bollandia antipathicola	0	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	1	1	0	0	0
Brachysyllis infuscata	0	1	0	3	1	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	3	3	3	0	0	1	?	?	?	0
Branchiosyllis oculata	0	1	1	0	1	0	1	?	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	1	0	1	0	0	1	0
Brania pusilla	0	1	0	1	1	0	0	1	0	0	0	0	0	0	2	0	0	0	0	0	0	1	1	1	0	0	0	0	2	0	0
Cicese sphaerosylliphormis	0	1	0	1	1	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	1	1	1	0	0	0	0	2	0	0
Clavisyllis alternata	1	1	?	0	1	0	1	0	0	0	0	0	0	0	4	1	0	0	0	0	0	0	0	0	0	1	1	?	?	?	0
Dentatisyllis mortoni	0	1	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	1	0	1	0	0	1	0
Dioplosyllis cirrosa	0	1	0	3	1	0	1	0	0	0	2	0	0	0	0	0	1	0	0	0	0	3	3	3	0	0	1	1	0	0	0
Epigamia labordai	1	1	0	0	1	0	0	0	1	0	-	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	1	?	?	?	0
Erinaceusyllis serratosetosa	0	0	0	1	1	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	1	1	1	0	0	0	0	2	0	0
Eurysyllis tuberculata	0	1	1	1	1	0	0	0	0	0	0	1	0	0	5	0	0	1	1	1	0	1	1	1	0	0	1	1	5	1	0
Eusyllis blomstrandi	0	1	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	1	0	1	0	0	0	0
Exogone naidina	0	0	0	2	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	2	2	2	0	0	0	0	1	0	0
Geminosyllis ohma	0	1	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	1	0	1	0	0	1	0
Haplosyllides floridana	0	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0
Haplosyllis spongicola	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	1	0	1	0	0	1	0
Imajimaea zonata	1	1	0	0	1	0	0	0	1	0	-	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	1	1	0	0	0
Inermosyllis balearica	0	1	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	1	1	0	1	0	0	1	0
Karroonsyllis exogoneformis	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	1	1	0	0	1	1	0	1	0
Lamellisyllis comans	1	1	?	0	1	0	1	0	0	0	0	0	0	0	4	1	0	0	0	0	0	0	0	0	0	1	1	1	4	?	0
Levidorum hartmanae	0	-	-	-	1	0	0	0	1	0	-	0	0	1	-	0	0	-	-	-	-	-	-	-	-	-	-	-	-	-	0
Miscellania dentata	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	1	0	0	0
Murrindisyllis kooromundrola	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	3	1	0	0	0	0	0	0	0
Myrianida prolifera	1	1	0	0	1	0	0	0	1	0	-	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	1	0	0	0	0
Neopetitia amphophthalma	0	1	0	0	1	0	1	0	0	0	2	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0
Nooralia bulgannabouyanga	0	1	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0
Nuchalosyllis lamellicornis	1	1	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	1	1	1	?	?	?	0
Nudisyllis pulligera	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0
Odontosyllis fulgurans	0	1	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	1	0	0	0	0
Opisthodonta morena	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0
Opisthosyllis brunnea	0	1	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	1	0	1	0	0	1	0
hydrozoicola	1	1	0	0	1	0	0	0	1	0	-	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	1	0	0	0	0
Palposyllis prosostoma	0	1	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	1	0	0	1	0	0	0	0
Paraehlersia ferrugina	0	1	2	0	1	0	1	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	1	0	1	0	0	2	0
Paraexogone hebes	0	0	0	2	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	2	2	2	0	0	0	0	1	0	0
Parahaplosyllis brevicirra	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	1	1	0	0	1	?	?	?	0
Paraopisthosyllis ornaticirra	0	1	0	1	1	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	1	1	1	1	1	0	0	0
Parapionosyllis minuta	0	0	0	1	1	0	0	1	0	0	0	0	0	0	2	0	0	0	0	0	0	1	1	1	0	0	0	0	2	0	0
Paraproceraea tamana	1	1	0	0	1	0	0	0	1	0	-	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	1	?	?	0	0
Paraprocerastea crocantinae	?	1	0	0	1	0	0	0	1	0	-	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	1	1	0	0	0
Parasphaerosyllis indica	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	1	0	1	1	1	0	0	0	0	1	0	1	0	0	1	0
Pionosyllis enigmatica	0	1	0	0	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0
Plakosyllis brevipes	0	1	1	1	1	0	0	0	0	0	0	1	0	0	5	0	0	1	1	1	0	1	1	1	0	0	1	1	5	1	0
Planicirrata proceraeae	1	1	0	0	1	0	0	0	1	0	-	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	1	?	?	?	0
Proceraea picta	1	1	0	0	1	0	0	0	1	0	-	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	1	1	0	0	0
Procerastea halleziana	1	1	0	0	1	0	0	0	1	0	-	0	0	1	-	0	0	-	-	-	-	-	-	-	-	-	-	1	0	-	0
Proshaerosyllis xarifae	0	0	0	1	1	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	1	1	1	0	0	0	1	2	0	0
Psammosyllis wui	0	1	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0
Rhopalosyllis hamulifera	0	1	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	1	1	0	0	1	1	0	1	0
Salvatoria clavata	0	1	0	1	1	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	1	1	1	1	0	0	1	2	0	0
Sphaerosyllis hystrix	0	0	0	1	1	0	0	1	0	0	0	0	0	0	2	0	0	0	0	0	0	1	1	1	0	0	0	1	2	0	0
Streptodontha pterochaeta	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	?	?	?	1
Streptospinigera heterosetosa	0	1	0	1	1	0	0	0	0	0	1	0	1	0	0	0	0	0	1	1	1	1	0	0	1	0	1	0	0	0	1
Streptosyllis websteri	0	1	0	1	1	0	0	0	0	0	1	0	1	0	0	0	0	0	1	1	0	1	0	0	1	0	1	0	0	0	1
Syllides japonicus	0	1	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	1	1	0	0	1	0	1	0	0	0	0
Syllis prolifera	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	1	0	1	0	0	1	0
Trypanosyllis aeolis	0	1	1	0	1	0	1	0	0	0	0	1	0	0	0	0	0	1	1	1	0	0	0	0	1	0	1	0	0	1	0
Virchowia clavata	1	1	0	0	1	0	0	0	1	0	-	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	0	0	0
Xenosyllis scabra	0	1	1	1	1	0	0	0	0	0	0	1	0	0	0	0	0	1	1	1	0	1	1	1	0	0	1	1	0	2	0

Taxa/Characters									7										8										9			
Pisione longispinulata	0	0	1	0	1	1	0	0	-	-	0	1	0	0	1	0	1	0	-	1	0	-	0	0	1	1	0	-	-	0	-
Nereis virens	0	0	0	-	-	-	0	0	-	-	0	0	0	0	0	0	1	0	-	1	0	-	0	0	1	0	0	-	-	0	-
Chrysopetalum maculata	0	0	0	-	-	-	0	0	-	-	0	0	0	0	1	0	0	1	1	0	1	1	0	0	1	0	0	-	-	0	-
Sphaerodoropsis anae	0	0	0	-	-	-	0	0	-	-	0	0	0	0	1	0	0	1	1	0	1	1	0	0	1	1	1	0	0	?	1
Alcyonosyllis phili	0	0	0	-	-	-	0	0	-	-	1	1	0	0	-	0	1	1	1	1	1	1	0	0	0	1	1	0	1	1	0
Amblyosyllis speciosa	0	0	0	-	-	-	0	0	-	-	0	0	0	0	1	0	0	1	1	0	1	1	0	0	1	1	1	1	0	1	0
Anguillosyllis capensis	0	0	1	1	?	1	0	1	0	0	0	0	0	0	1	0	1	0	-	1	0	-	0	0	1	1	1	1	1	1	0
Anoplosyllis edentulus	2	0	1	0	1	1	0	0	-	-	0	0	0	0	1	0	1	1	1	1	1	1	0	0	1	1	1	1	0	1	1
Astreptosyllis acrassiseta	2	0	1	0	0	1	1	1	0	1	0	0	1	0	1	0	1	1	0	1	1	0	0	1	1	1	1	1	2	1	0
Bollandia antipathicola	0	0	0	-	-	-	0	0	-	-	1	1	0	-	-	0	1	0	-	1	0	-	0	0	0	1	1	1	0	?	0
Brachysyllis infuscata	0	0	0	-	-	-	0	0	-	-	0	0	0	0	1	0	0	1	1	0	1	1	0	0	1	1	1	0	0	1	0
Branchiosyllis oculata	0	0	0	-	-	-	0	0	-	-	0	0	0	0	0	0	1	0	-	1	0	-	0	0	0	1	1	0	1	1	0
Brania pusilla	2	1	1	0	1	1	0	1	1	1	0	0	0	0	1	0	0	1	1	0	1	1	1	0	1	1	1	0	0	1	0
Cicese sphaerosylliphormis	1	0	1	0	1	1	0	1	0	0	0	0	0	0	1	0	0	1	1	0	1	1	0	0	1	1	1	1	1	1	0
Clavisyllis alternata	0	0	0	-	-	-	0	0	-	-	0	0	0	0	0	0	0	1	1	0	1	1	0	0	1	1	1	1	1	1	0
Dentatisyllis mortoni	1	0	1	1	1	0	0	1	1	0	0	0	0	0	1	1	0	1	1	0	1	1	0	0	1	1	1	0	1	1	0
Dioplosyllis cirrosa	0	0	0	-	-	-	0	0	-	-	0	0	0	0	0	0	0	1	1	0	1	1	0	0	1	1	1	0	1	1	0
Epigamia labordai	0	0	1	0	1	2	0	0	-	-	0	0	0	0	0	0	0	1	2	0	1	2	0	0	1	1	1	1	1	1	0
Erinaceusyllis serratosetosa	1	0	1	0	0	1	0	1	0	1	0	0	0	0	1	1	1	0	-	1	0	-	0	0	1	1	1	1	1	1	0
Eurysyllis tuberculata	1	0	0	-	-	-	0	1	0	1	0	0	0	0	0	0	1	0	-	1	0	-	0	0	1	1	1	0	1	1	0
Eusyllis blomstrandi	2	0	1	1	?	1	0	1	?	0	0	0	0	0	1	0	0	1	0	0	1	2	0	0	1	1	1	0	2	1	0
Exogone naidina	2	0	1	0	1	1	0	1	0	0	0	0	0	0	1	1	0	1	2	0	1	2	0	0	1	1	1	0	0	1	0
Geminosyllis ohma	2	0	0	-	-	-	0	1	0	0	1	1	0	-	-	-	0	1	0	0	1	0	0	0	1	1	1	0	2	1	0
Haplosyllides floridana	0	0	0	-	-	-	0	0	-	-	1	1	0	-	-	-	0	1	0	0	1	0	0	0	0	1	1	0	1	1	0
Haplosyllis spongicola	2	0	0	-	-	-	0	0	-	-	1	1	0	-	-	-	0	1	0	0	1	0	0	0	0	1	1	0	1	1	0
Imajimaea zonata	0	0	1	0	1	2	0	0	-	-	0	0	0	0	0	0	0	1	2	0	1	2	0	0	1	1	1	1	0	1	0
Inermosyllis balearica	1	0	1	1	1	0	0	1	1	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0	1	1	1	0	2	1	0
Karroonsyllis exogoneformis	2	1	1	1	1	0	0	1	0	0	0	0	0	0	1	0	0	1	1	0	1	1	0	0	1	1	1	0	0	1	0
Lamellisyllis comans	0	0	1	1	0	1	0	1	1	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0	1	1	1	1	1	1	0
Levidorum hartmanae	0	0	0	-	-	-	0	0	-	-	1	1	0	-	-	-	0	1	2	0	1	2	0	0	1	1	1	0	0	1	0
Miscellania dentata	1	0	1	0	1	1	0	1	1	1	0	0	0	0	1	0	1	0	-	1	0	-	0	0	1	1	1	1	0	1	0
Murrindisyllis kooromundrola	0	0	1	0	0	1	0	1	0	1	0	1	0	0	0	0	1	0	-	1	0	-	0	0	1	1	1	0	2	1	1
Myrianida prolifera	0	0	1	0	1	2	0	0	-	-	0	0	0	0	0	0	0	1	2	0	1	2	0	0	1	1	1	1	0	1	0
Neopetitia amphophthalma	0	0	1	0	1	0	0	1	0	0	0	0	0	0	1	0	0	1	1	0	1	1	0	0	1	1	1	1	0	1	0
Nooralia bulgannabouyanga	1	0	1	0	1	1	0	0	-	-	0	0	1	0	1	0	1	1	0	1	1	0	0	0	1	1	1	0	0	1	0
Nuchalosyllis lamellicornis	0	0	0	-	-	-	0	0	-	-	0	0	0	0	0	0	1	0	-	1	0	-	0	0	1	1	1	0	1	1	1
Nudisyllis pulligera	1	0	1	1	?	0	0	?	?	?	0	0	0	1	1	0	0	1	1	1	0	-	0	0	1	1	1	0	0	1	1
Odontosyllis fulgurans	1	0	1	1	1	0	0	1	1	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	1	1	1	0	1	1	1
Opisthodonta morena	2	0	0	-	-	-	0	0	-	-	0	0	0	0	1	1	0	1	0	0	1	2	0	0	1	1	1	0	2	1	0
Opisthosyllis brunnea	2	1	1	1	1	1	0	1	1	1	0	0	0	0	0	0	0	1	1	1	0	-	0	0	1	1	1	0	2	1	0
hydrozoicola	0	0	1	0	1	2	0	0	-	-	0	1	0	0	0	0	0	1	2	0	1	2	0	0	1	1	1	1	0	1	0
Palposyllis prosostoma	0	0	1	1	1	1	0	1	0	0	0	0	0	0	0	0	1	1	1	1	1	1	0	0	1	1	1	0	1	1	0
Paraehlersia ferrugina	1	0	1	1	1	0	0	1	?	0	0	0	0	1	1	1	0	1	0	0	1	2	0	0	1	1	1	0	2	1	0
Paraexogone hebes	2	0	1	0	1	0	0	1	0	0	0	0	0	0	1	0	0	1	1	0	1	1	0	0	1	1	1	0	0	1	0
Parahaplosyllis brevicirra	0	0	1	1	0	0	0	0	-	-	1	1	0	-	-	-	0	1	1	0	1	1	0	0	0	1	1	0	1	1	0
Paraopisthosyllis ornaticirra	2	0	1	1	1	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1	1	1	0	1	1	0
Parapionosyllis minuta	2	1	1	0	1	1	0	1	0	1	0	0	0	0	1	0	1	1	1	1	1	1	1	0	1	1	1	0	0	1	0
Paraproceraea tamana	0	0	1	0	1	2	0	0	-	-	0	0	0	0	0	0	0	1	2	0	1	2	0	0	1	1	1	1	0	1	0
Paraprocerastea crocantinae	0	0	1	0	1	2	0	0	-	-	1	1	0	-	-	-	0	1	2	0	1	2	0	0	0	1	1	1	1	1	0
Parasphaerosyllis indica	0	0	1	1	?	1	0	1	0	?	0	0	0	0	1	0	0	1	0	0	1	0	0	0	1	1	1	0	0	1	0
Pionosyllis enigmatica	0	0	1	1	?	0	0	1	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0	1	1	1	0	2	1	0
Plakosyllis brevipes	0	0	1	1	0	1	0	1	0	1	0	0	0	0	0	0	1	0	-	1	0	-	0	0	1	1	1	1	0	1	0
Planicirrata proceraeae	0	0	1	0	1	2	0	0	-	-	0	0	0	0	0	0	0	1	2	0	1	2	0	0	0	1	1	1	1	1	0
Proceraea picta	0	0	1	0	1	2	0	0	-	-	0	0	0	0	0	0	0	1	2	0	1	2	0	0	1	1	1	1	1	1	0
Procerastea halleziana	0	0	1	0	1	2	0	0	-	-	0	1	0	0	0	0	0	1	2	0	1	2	0	0	0	1	1	1	0	1	0
Proshaerosyllis xarifae	1	0	1	0	0	1	0	1	0	1	0	0	0	0	1	0	1	0	-	1	0	-	0	0	1	1	1	1	1	1	0
Psammosyllis wui	2	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	1	1	0	0	1	1	1	0	0	1	0
Rhopalosyllis hamulifera	0	0	1	1	0	1	0	1	0	0	0	1	0	0	0	0	0	1	0	0	1	0	0	0	0	1	1	1	0	1	0
Salvatoria clavata	1	0	1	0	1	0	0	1	1	0	0	0	0	0	1	0	0	1	1	0	1	1	0	0	1	1	1	1	0	1	0
Sphaerosyllis hystrix	2	0	1	0	1	1	0	1	0	1	0	0	0	1	1	0	1	1	1	1	0	-	0	0	1	1	1	0	0	1	0
Streptodontha pterochaeta	2	0	1	1	0	1	0	0	-	-	0	0	0	0	0	0	0	1	2	0	1	2	0	0	1	1	1	0	2	1	0
Streptospinigera heterosetosa	2	0	1	0	1	1	1	0	-	-	0	0	1	0	1	1	1	0	-	1	0	-	0	0	1	1	1	1	1	1	0
Streptosyllis websteri	2	0	1	0	1	1	1	0	-	-	0	0	1	0	1	0	0	1	0	0	1	0	0	1	1	1	1	1	1	1	1
Syllides japonicus	1	0	1	0	1	0	0	0	-	-	0	0	0	0	1	0	0	1	0	0	1	0	0	0	1	1	1	1	1	1	1
Syllis prolifera	2	1	1	1	1	0	0	1	1	0	0	0	0	0	1	0	0	1	1	0	1	1	0	0	1	1	1	0	2	1	0
Trypanosyllis aeolis	0	0	0	-	-	-	0	0	-	-	0	0	0	0	1	0	0	1	1	0	1	1	0	0	1	1	1	0	2	1	0
Virchowia clavata	0	0	1	0	1	2	0	0	-	-	0	0	0	0	0	0	0	1	2	0	1	2	0	0	1	1	1	1	0	1	0
Xenosyllis scabra	0	0	0	-	-	-	0	1	0	0	0	0	0	0	1	0	0	1	1	1	1	1	0	0	1	1	1	0	0	1	0

Taxa/Characters								10										11		
Pisione longispinulata	0	0	1	0	0	-	-	0	0	0	-	-	-	-	0	0	-	0
Nereis virens	0	0	1	0	0	-	-	0	0	1	0	2	-	-	0	0	-	0
Chrysopetalum maculata	0	0	1	0	0	-	-	0	0	0	-	-	-	-	0	0	-	0
Sphaerodoropsis anae	0	0	0	0	0	-	-	0	0	0	-	-	-	-	0	0	-	0
Alcyonosyllis phili	0	0	0	1	1	0	0	0	0	1	1	1	1	1	0	0	-	0
Amblyosyllis speciosa	1	2	0	1	0	-	-	1	0	1	0	2	-	-	0	1	2	0
Anguillosyllis capensis	0	0	0	0	0	-	-	0	0	?	?	?	?	?	?	?	?	0
Anoplosyllis edentulus	0	0	0	0	0	-	-	0	0	0	-	-	-	-	1	1	2	0
Astreptosyllis acrassiseta	0	0	0	0	0	-	-	0	0	?	?	?	?	?	?	?	?	0
Bollandia antipathicola	1	2	0	0	0	-	-	0	0	0	-	-	-	-	?	?	?	0
Brachysyllis infuscata	0	0	0	1	1	0	0	0	1	1	0	2	-	-	0	0	-	0
Branchiosyllis oculata	0	0	0	1	1	0	0	0	0	1	1	1	1	0	0	0	-	0
Brania pusilla	0	0	0	1	1	0	0	0	0	1	0	2	-	-	1	1	1	0
Cicese sphaerosylliphormis	0	1	0	1	0	1	0	0	0	1	0	2	-	-	0	?	0	0
Clavisyllis alternata	0	0	0	1	1	0	0	0	0	?	?	?	?	?	?	?	?	0
Dentatisyllis mortoni	0	0	0	1	1	0	0	1	0	0	-	-	-	-	1	1	4	0
Dioplosyllis cirrosa	0	0	0	1	1	0	0	0	1	?	?	?	?	?	?	?	?	0
Epigamia labordai	1	2	0	1	0	-	-	1	0	1	0	2	-	-	0	0	-	0
Erinaceusyllis serratosetosa	0	1	0	1	1	1	0	0	0	1	0	2	-	-	0	1	0	0
Eurysyllis tuberculata	0	0	0	1	1	0	0	1	0	1	1	1	1	0	0	0	-	0
Eusyllis blomstrandi	0	0	0	1	1	0	0	0	1	1	0	2	-	-	0	0	-	1
Exogone naidina	0	0	0	1	1	0	0	0	0	1	0	2	-	-	1	1	1	0
Geminosyllis ohma	0	0	0	1	1	0	0	1	0	?	?	?	?	?	?	?	?	0
Haplosyllides floridana	0	0	0	1	1	0	0	0	0	1	1	1	1	0	0	0	-	0
Haplosyllis spongicola	0	0	0	1	1	0	0	0	0	1	1	1	1	0	0	0	-	0
Imajimaea zonata	1	2	0	1	0	-	-	1	0	1	1	0	?	0	0	0	-	0
Inermosyllis balearica	0	0	0	0	0	-	-	0	0	?	?	?	?	?	?	?	?	0
Karroonsyllis exogoneformis	0	0	0	1	1	0	0	0	0	?	?	?	?	?	?	?	?	0
Lamellisyllis comans	0	0	0	1	1	0	?	0	0	?	?	?	?	?	?	?	?	0
Levidorum hartmanae	1	2	0	1	0	-	-	1	0	1	1	0	?	0	0	0	-	0
Miscellania dentata	0	0	0	1	1	0	0	0	1	?	?	?	?	?	?	?	?	0
Murrindisyllis kooromundrola	0	1	0	0	0	-	-	0	0	?	?	?	?	?	?	?	?	0
Myrianida prolifera	1	2	0	1	0	-	-	1	0	1	1	-	0	0	0	1	3	0
Neopetitia amphophthalma	0	0	0	1	1	0	0	0	0	0	-	-	-	-	?	?	?	0
Nooralia bulgannabouyanga	0	0	0	0	0	-	-	0	0	1	0	2	-	-	0	1	0	0
Nuchalosyllis lamellicornis	0	0	0	1	1	0	0	?	?	1	1	1	1	0	0	0	-	0
Nudisyllis pulligera	0	0	0	1	1	0	0	0	0	1	0	2	-	-	1	0	-	0
Odontosyllis fulgurans	0	0	0	1	0	-	-	0	1	1	0	2	-	-	0	0	-	0
Opisthodonta morena	0	0	0	1	1	0	1	0	0	1	0	2	-	-	0	0	-	0
Opisthosyllis brunnea	0	0	0	1	1	0	1	0	0	1	1	1	1	0	0	0	-	0
Pachiprocerastea hydrozoicola	1	2	0	1	0	-	-	1	0	1	1	0	0	0	0	0	-	0
Palposyllis prosostoma	0	0	0	1	1	0	0	0	0	?	?	?	?	?	?	?	?	0
Paraehlersia ferrugina	0	0	0	1	1	0	0	0	0	1	0	2	-	-	0	0	-	1
Paraexogone hebes	0	0	0	1	1	0	0	0	0	0	-	-	-	-	1	1	4	0
Parahaplosyllis brevicirra	1	2	0	1	1	0	0	1	0	1	1	1	1	1	0	0	-	0
Paraopisthosyllis ornaticirra	0	1	0	1	1	0	1	0	0	?	?	?	?	?	?	?	?	0
Parapionosyllis minuta	0	0	0	1	1	0	0	0	0	1	0	2	-	-	1	1	1	0
Paraproceraea tamana	1	2	0	1	0	-	-	1	0	?	?	?	?	?	?	?	?	0
Paraprocerastea crocantinae	1	2	0	1	0	-	-	1	0	?	?	?	?	?	?	?	?	0
Parasphaerosyllis indica	0	0	0	1	1	0	0	0	0	1	1	1	1	?	0	0	-	0
Pionosyllis enigmatica	0	0	0	1	1	0	0	0	0	1	0	2	-	-	0	0	-	0
Plakosyllis brevipes	0	0	0	1	1	0	0	0	0	1	1	1	1	0	0	0	-	0
Planicirrata proceraeae	1	2	0	1	0	-	-	1	0	1	1	0	?	0	0	0	-	0
Proceraea picta	1	2	0	1	0	-	-	1	0	1	1	0	0	0	0	1	3	0
Procerastea halleziana	1	2	0	1	0	-	-	1	0	1	1	0	0	0	0	1	3	0
Proshaerosyllis xarifae	0	1	0	1	1	1	1	0	0	1	0	2	-	-	0	1	0	0
Psammosyllis wui	0	0	0	1	1	0	1	0	0	?	?	?	?	?	?	?	?	0
Rhopalosyllis hamulifera	0	1	0	1	1	0	0	0	0	1	1	1	1	?	0	0	-	0
Salvatoria clavata	0	1	0	1	1	1	0	0	0	1	0	2	-	-	0	1	0	0
Sphaerosyllis hystrix	0	0	0	1	1	0	0	0	0	1	0	2	-	-	1	1	1	0
Streptodontha pterochaeta	0	0	0	1	1	0	1	0	0	1	0	2	-	-	0	0	-	0
Streptospinigera heterosetosa	0	0	0	0	0	-	-	0	0	1	0	2	-	-	0	0	-	0
Streptosyllis websteri	0	1	0	0	0	-	-	0	0	1	0	2	-	-	0	0	-	0
Syllides japonicus	0	0	0	0	0	-	-	0	0	1	0	2	-	-	?	1	1	0
Syllis prolifera	0	0	0	1	1	0	0	0	0	1	1	1	1	0	0	0	-	0
Trypanosyllis aeolis	0	0	0	1	0	-	-	1	0	1	1	1	1	1	0	0	-	0
Virchowia clavata	1	2	0	1	0	-	-	1	0	1	1	0	0	0	0	0	-	0
Xenosyllis scabra	0	0	0	0	0	-	-	0	0	1	?	?	?	?	?	?	?	0

Agradecemos a las revistas Scientia Marina, Zootaxa, Revista de Biología Tropical y Cladistics la posibilidad de incorporar los archivos “pdf” de los artículos ya publicados. El artículo publicado en Cladistics incorporado a esta tesis doctoral es la versión “*early online*” pudiendo presentar diferencias en la numeración de páginas una vez publicado en soporte papel.

El pie de figura de la página 76 de esta tesis doctoral (p. 736, Rev. Biol. Trop., 54) corresponde a la especie *Syllis botosaneanui*.

La foto de la portada corresponde a un *Trypanosyllis* sp., modificada de E. Nishi. El dibujo de la contraportada es un *Trypanosyllis* sp., por Yolanda Lucas.